On the Morphology of the Cranial Muscles in Some Vertebrates.

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With 100 Text-figures.

In the following paper I have described and compared the development of some of the cranial muscles in Scyllium canicula, Squalus acanthias, Acipenser sturio, Lepidosteus osseus, Amia calva, Salmo fario, Ceratodus Forsteri, Triton cristatus, Rana temporaria, Alytes obstetricans, Bufo lentiginosus, Pelobates fuscus, Chrysemys marginata, Lacerta agilis, chick, rabbit, and pig.

The object has been to determine as far as possible the morphology of the muscles, and so to deduce a morphological classification of the motor nuclei of the cranial nerves, more especially in mammals and man.

A subsidiary object has been to ascertain what evidence is afforded by these muscles in regard to the speculations of zoologists on the phylogenetic relations of the various vertebrate groups.

The paper is a sequel to one previously published on some of the cranial muscles of Sauropsida.

The adult anatomy of the muscles has been described by Vetter, Fürbringer, Pollard, McMurrich, Allis, Jaquet, Drüner, Ecker and Gaupp, Mivart, Krause, and others referred to in the paper. In the majority of cases observation of the development of the muscles merely serves to support deductions as to their homologies already made from consideration

of their adult forms, but in some cases it suggests corrections.

In the case of Lepidosteus only the hypobranchial muscles have been described—by Fürbinger, and the names for other muscles have been as far as possible those used by Vetter and Allis in Ganoids and Teleostei. The cranial muscles of Polypterus have been described by Pollard, and the hypobranchial muscles by Fürbringer. They did not state the species examined. Those of Polypterus senegalus (specimens $7\frac{1}{2}$ to $9\frac{1}{2}$ cm. long) differ in a few particulars from the descriptions given by those authors. The cranial muscles of Salmo fario have not hitherto been described, but the researches of Vetter in other Teleostei made identification and nomenclature possible.

Van Wijhe described the early stages of the development of the cranial muscles of Scyllium; and Miss Platt those of Necturus; observations otherwise have been limited to the development of individual muscles or muscle-groups.

The nomenclature employed by previous writers has, in general, been followed. In cases where different names have been applied to homologous muscles in related animals a choice has been made, and this has necessitated some changes.

The paper is divided into the following sections: (1) The segmentation of the head; (2) mandibular muscles; (3) hyoid muscles; (4) eye muscles of the rabbit; (5) branchial muscles; (6) œsophageal, laryngeal, and pharyngeal muscles; (7) muscles derived from trunk myotomes passing to the upper ends of the branchial bars; (8) hypobranchial spinal muscles; (9) lingual muscles; (10) some phylogenetic speculations; (11) on Fürbringer's theory of the skull; (12) a suggested morphological classification of the motor centres of the mid- and hind-brain in man.

The Segmentation of the Head.

In the body region of Scyllium embryos it is found that there is an unsegmented part below enclosing the cœlom, and

a segmented part above, the somite, which subsequently separates from the dorsal edge of the cœlom and develops into myotome and sclerotome.

In the head the conditions in the mandibular and hyoid segments are different from those in the branchial segments; in the latter the lateral plates of mesoderm are at first continuous ventrally with the wall of the pericardium or cephalic cœlom[1] (Text-fig. 2); in the mandibular and hyoid segments
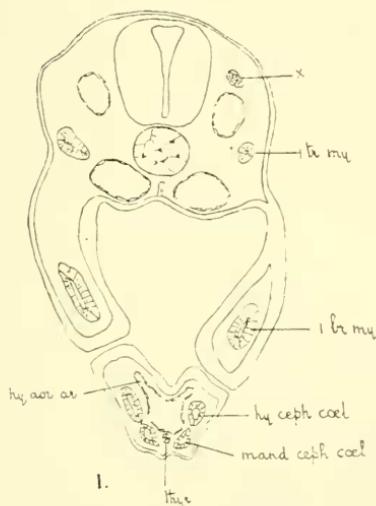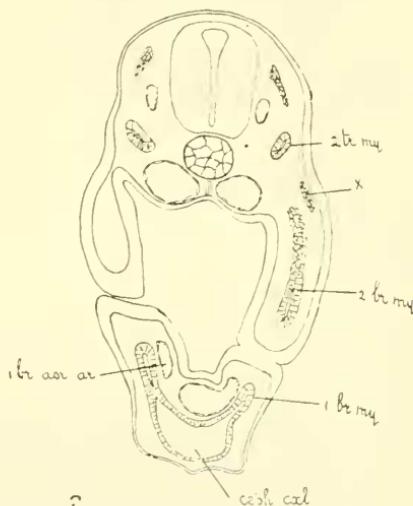
Text-figs. 1 and 2.—Scyllium, embryo 7 mm., transverse sections. Text-fig. 1 is the more anterior.

the lateral plates of mesoderm are continuous ventrally with the walls of the mandibular and hyoid sections of the cephalic cœlom. These differ from the branchial sections in that no communication from side to side takes place (Text-fig. 1). In the rabbit, however (Text-fig. 76), the cephalic cœlom is continuous from side to side in the mandibular and hyoid segments, just as it is in the branchial segments.

[1] The latter name is perhaps preferable, as probably the heart originally lay behind the branchial region.

[2] For reference letters on Text-figures see p. 314.

The lateral plate of the hyoid segment extends upwards and forwards lateral to the alimentary canal between the first and second gill-clefts; its upper end in $6\frac{1}{2}$ and 7 mm. embryos (= stages H and I of Balfour) is continuous above with the "fourth myotome" of van Wijhe.

Van Wijhe says that the "fourth myotome" in stage J is separated from the lateral plate and is very rudimentary, also that it atrophies towards the end of that period; further, that "bis in dieselbe Höhe aber mehr lateral verlangen sich in spateren Stadien die Wände der jetzigen Hyoidhöhle. Mit dieser Verlängerung darf das vierte Myotome nicht verwechselt werden." The Anlage of the rectus externus, regarded by van Wijhe as the third myotome, was stated to be continuous in stage I with the solid cell mass in the hyoid arch, and in stage J to be no longer so.

In the embryos of $6\frac{1}{2}$ and 7 mm. in length (= stages H and I) examined, it was found that the Anlage of the rectus externus was continuous behind with the upper end of the epithelium-lined cavity in the hyoid arch, i. e. with the fourth myotome of van Wijhe. In embryos of 9 mm. (Text-fig. 3) and 10 mm. it was found that the epithelial walls of the hyoid cavity had come together, so that the cavity had disappeared, that the now solid cell column had extended upwards, and that the Anlage of the rectus externus was continuous behind with this cell column some little distance from its upper end, at a site corresponding with the original upper end of the hyoid cavity. No trace of a separated "fourth myotome" was seen. It is therefore possible, on the analogy of what takes place in the trunk, to regard the whole of the "lateral plate" and "fourth myotome"—which do not become separate—as together forming the hyoid myotome.

This theory is supported by the difficulty of finding any structure in the body region which is homologous with the lateral plates of the head. Ziegler was of opinion that they were homologous with the "Urwirbelkommunikation" (of Rabl), the "Ursegmentsteil" (of Felix). But it is scarcely possible that epithelial structures of the head, which develop

into muscles, can be homologous with epithelial structures in the body, which are the " Mutterboden für den verschiedenen Harnkanälchen " (Felix). Nor do the lateral plates of the head appear to be homologous with the " Seitenplatten " (of Felix) in the body, for this term denotes the epithelium lining the cœlom.

The Anlage of the rectus externus may be regarded as a

TEXT-FIG. 3.

3.
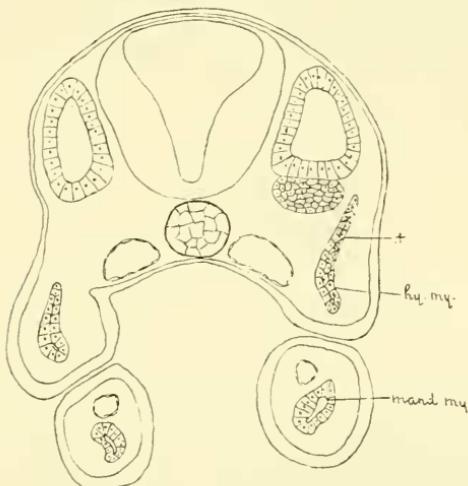
Scyllium, embryo 9 mm., transverse section. The line attached to the mark * shows the point of junction of the Anlage of the external rectus with the hyoid myotome.

very early anterior prolongation of the upper end of the hyoid myotome.

Ziegler was of opinion that the eye-muscles gave no evidence of the primary segmentation of the head, but attributed the Anlage of the rectus externus to the mandibular segment.

The Anlage of the obliquus superior was regarded by van Wijhe as the second myotome of the head. On the analogy of the rectus externus it may be looked upon as simply a forward projection of the upper end of the mandibular

myotome. Both these Anlagen are anterior projections from
the upper ends of their respective myotomes, to add to the
musculature of the eye, which is primarily formed from the
pre-mandibular segment.

As above stated, the lateral plate of the mandibular
segment, which is serially homologous with that in the hyoid
segment, may be regarded as the myotome of that segment.

In the case of the five branchial segments, the epithelium-
lined cavities—the lateral plates of van Wijhe—are con-
tinuous below with the cephalic cœlom. Above, they are

TEXT-FIG. 4.
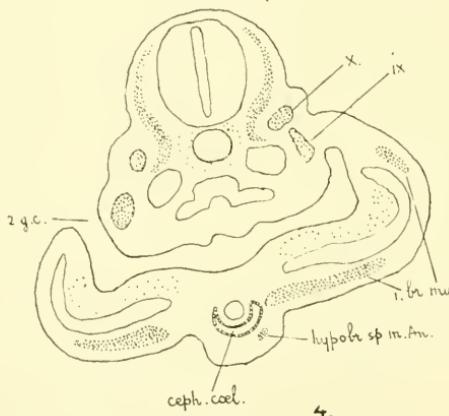
Scyllium, embryo 14 mm., transverse section.

stated by van Wijhe to be continuous with myotomes—his
sixth, seventh, eighth, and ninth. These myotomes were
stated to separate from the lateral plates, and to undergo
various changes, the fifth atrophying, the sixth becoming
very rudimentary, and the seventh, eighth, and ninth forming
"Vom Schädel zum Schultergürtel ziehende Muskeln nebst
dem vordersten Theile des sterno-hyoideus." In regard to
this asserted continuity between the myotomes and lateral
plates, it is noteworthy that Ziegler says it is "schwierig den
unten Ursprung des Ursegments mit dem oben sichbaren
Myotom in Verbindung zu bringen, und dies ist bis jezt
keinem einzigen Forscher in der richtigen Weise gelungen."

It might be expected that if the lateral plates are the splanchnic elements of myotomes above, their relation to the latter would be constant. But this is not so; for instance, in the figure given by Ziegler of a 6·5 mm. Torpedo embryo, two lateral plates (those of the second and third branchial arches) lie beneath three myotomes—his fifth, sixth, and seventh (= sixth, seventh, and eighth of van Wijhe), and the lateral plate of the fourth branchial arch lies below his eighth. In Ceratodus, according to Greil, the lateral plates of the first three branchial segments are continuous above with one (the first) myotome, and those of the fourth and fifth branchial segments are continuous above with one myotome (the second). In Rana esculenta, with five to six somites (Corning, '99, Taf. ix, figs. 7 and 11), the lateral plates of the first and second branchial segments lie in front of the first myotome. To this may be added that in rabbit embryos 3 mm. long (Text-fig. 78) the first branchial lateral plate lies in front of the first trunk myotome, and the second and third branchial lateral plates (as yet not separated) lie beneath the first trunk myotome.

Secondly, it might be expected that the lateral plate would in all animals be at first continuous with a myotome above, but in Necturus embryos (Text-figs. 51–53) and rabbit embryos (Text-fig. 78) it is not possible to see any continuity.

Both these points have been emphasised by Agar in a recent criticism of the theory of van Wijhe. Agar's theory is that the fourth somite of van Wijhe represents the condensed somatic portion of the hinder palingenetic head somites, and he points out that some observers have described more than one somite in this situation, e. g. Brauss, two in Spinax, and Miss Platt, three in Acanthias. The difficulty in accepting this theory is that, as above stated, this fourth somite is, in Scyllium, continuous with the lateral plate of the hyoid segment.

Ziegler throws doubt on the existence of van Wijhe's fifth myotome—the one which lies above the first branchial segment—on the ground that in Torpedo its cavity is no more

TEXT-FIG. 5.

5.
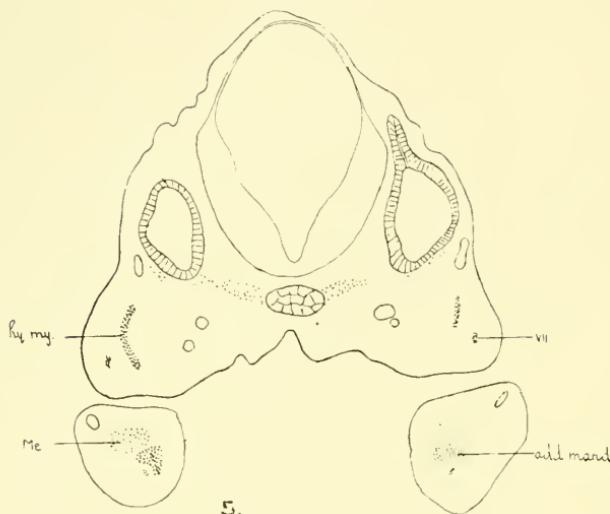
TEXT-FIG. 6.

6.
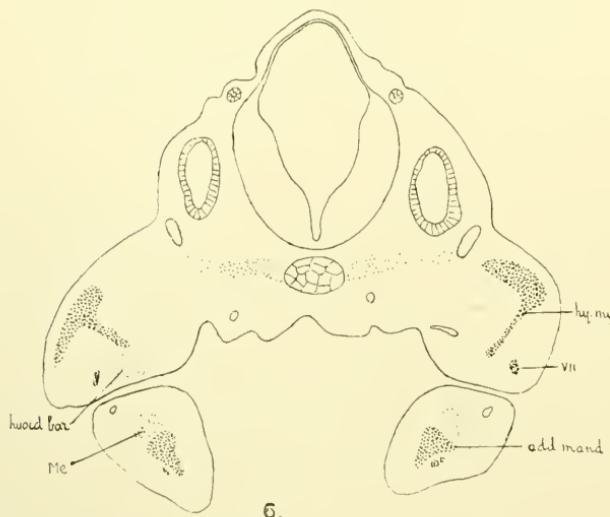
Text-figs. 5 and 6.—Scyllium, embryo 16 mm., transverse sec-
tions.   Text-fig. 5 is more anterior.   In the sections the right
side is slightly anterior to the left.

than a cleft, and that it quickly becomes rudimentary. He concludes that it is only a small cavity in the mesenchyme and of no theoretic importance. It is difficult to share this opinion, for the corresponding structure in Scyllium is lined by epithelial cells and closely resembles the next following myotome (Text-figs. 1 and 2).

Ziegler counts three myotomes in Torpedo (his fifth, sixth, and seventh) corresponding to three lateral plates, regards the vagus as a "zusammengesetzte Nervencomplex" corresponding to three segments, and is of opinion that it is in correspondence with this that the next following myotome (his eighth = van Wijhe's ninth) is the foremost to have any nerve-roots, an anterior one only. The difficulties in accepting such a view are: first, as stated above, the want of anterolateral correspondence between the myotomes and lateral plates; and secondly, in Scyllium, and probably also in Torpedo at a later stage, a fifth branchial lateral plate is formed, i. e. there would be an overlapping of the territories of the vagus and spinal roots.

Greil's views as to the nature of the mesoderm of the head of Ceratodus are very different from the foregoing. He holds that the musculature of the branchial region is derived from downgrowths of the first two myotomes, that in the first three branchial arches being derived from the first myotome, that in the fourth and fifth arches from the second myotome. The cells forming these downgrowths can be distinguished from the immediately subjacent lateral plates by the shape of their nuclei and by the later absorption of their yolk-granules. The downgrowths increase in vertical depth from behind forwards. The lateral plates of the branchial arches degenerate into connective tissue. The dorsal portions of the first three arches, i. e., those which are formed from the first myotome, develop dorsally into the levatores arcum branchialum and ventrally into the second and third interbranchiales and the ceratohyoideus; that of the fourth arch into the fourth levator and fourth interbranchialis; that of the fifth arch anteriorly into the dorso-laryngeus and the fifth inter-

branchialis, and posteriorly into the fifth levator and levator scapulæ. The musculature of the hyoid and mandibular arches cannot be regarded as derivations either of a somite or of a lateral plate; it never takes on lateral-plate characteristics.

A difficulty in accepting this theory is that it does not seem to be of general applicability in Vertebrates. Thus, as stated above, in the rabbit the lateral plate of the first branchial arch is in front of the first trunk myotome, and those of the second and third arches lie below the first trunk myotome; and there is a gap between the dorsal edges of the lateral plates of the second and third arches and the ventral edge of the first myotome. A difference in the shape of the cell-nuclei and in the rate of absorption of yolk-granules does not appear to be of sufficient importance to justify a separation into upper and lower portions of a structure which in other animals has been called lateral plate. As far as I have been able to observe, the ventral end of the lateral plate, taken in its usual sense, does not degenerate into connective tissue, but becomes converted into muscles.

These difficulties lead to the following theory of the segmentation of the head. It is probable that it originally consisted of five segments only—the premandibular, mandibular, hyoid, first branchial, second branchial—each having a myotome, which, in the case of the four latter, contains a slit-like, epithelium-lined cavity continuous with the cephalic cœlom below. To each myotome passed a nerve—the IIIrd, Vth, VIIth, IXth, and Xth.[1] The gill-clefts are intersegmental. New segments were added, one by one, behind the second branchial, the head extended back into the body-region, and

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[1] According to Neal ('98) only one encephalomere corresponds to the vagus—a fact which, if the encephalomeres have segmental, or rather inter-segmental, worth, agrees with the theory that the vagus is not a " zusammengesetzte Nervencomplex," but primarily, as regards its motor branches, of one segment only—the second branchial—and that additional branches were developed as the number of gill-clefts and branchial segments was added to.

the added myotomes necessarily lie beneath the anterior body myotomes, with their upper ends at varying distances from the ventral surface of the latter, with which they may or may not agree in antero-posterior extent. In Rana esculenta, with five to six somites, the most anterior trunk myotome lies above the third branchial, i. e. the first added myotome ; a little later there is a relative shifting forward of the trunk myotomes, so that the first trunk myotome comes to lie above the first branchial myotome (see Corning's figures, Taf. ix, figs. 7, 11, and 26). In Scyllium this overlapping is, secondarily, antedated in development, so that the first branchial myotome never lies in front of the first trunk myotome. In the rabbit it does so.

The backward growth of the head into the body by this process of metameric increase leads to the non-development of the cœlomic portion of the anterior trunk-somites. In Scyllium, for instance, the first four trunk-somites have no cœlomic portions.

In the head, as in the body, each myotome is at first an epithelium-lined cavity, which is continuous below with the cœlom. The differences between the myotomes of the body and those of the head are : (1) Whereas in the body the myotomes extend dorsally to the mid-dorsal line, and, subsequently, ventrally outside the somatopleure wall of the cœlom to the mid-ventral line, neither of these secondary phenomena takes place in the head ; (2) whereas the cœlom is large in the body and contains the alimentary canal and other viscera, it is small in the head and lies entirely ventral to the alimentary canal ; (3) in correlation with this the myotomes of the body lie, at first, dorso-lateral to the alimentary canal, those of the head lie dorso-lateral and lateral to it ; (4) the sclerotome elements of the body-myotomes are formed by ventromedial outgrowths, those of the head from scattered cells given off from the premandibular, mandibular, and hyoid myotomes. These differences are intimately associated with the development of gill-clefts and a cranium in the head, of viscera and a vertebral column in the body.

If, following Fürbringer, it be supposed that primitively the myotomes lay exclusively lateral to the chorda dorsalis, it would follow that they have taken different paths of development in the head and body, resulting in the conditions above stated.

According to the generally accepted theory, certain Selachii, e. g. Heptanchus, are the most primitive of gnathostome Vertebrates, in that they have the greatest number of branchial segments; and the lessened number of branchial segments in Teleostomi, Amphibia, and Dipnoi is due to a disappearance of the hinder ones. If, however, it be supposed that the original number of branchial segments was two, i. e. first and second, and that these were added to by a process of metameric increase, the interesting question arises as to the least number present in these Vertebrate groups, for this may be supposed to have been possessed by some primitive form. The Amphibia have four branchial segments, Dipnoi and most Teleostomi five (though Polypterus has only four), and most Elasmobranchs five, though they may have as many as seven. It may therefore be supposed that the original number present in Amphibia was added to in the other groups. This harmonises with the conclusion, stated later, that the condition of the muscles of the head in Amphibia is more primitive than in Dipnoi, Teleostomi, and Elasmobranchs.

The lessened number present in Sauropsida and Mammalia may be supposed to have resulted from reduction of the hinder of these four branchial segments. In the later stages of Reptiles, previously investigated, only two branchial myotomes were seen, but the early stages of Chrysemys marginata show four. In Gallus only two are present, even in the early stages. In Lepus only the first three are developed.

The cephalic cœlom disappears in the mandibular and hyoid segments early in development, and its walls develop into the intermandibularis and interhyoideus, which are at first continuous with the mandibular and hyoid myotomes. The lower ends of the branchial myotomes separate from the wall of the branchial portion of the cephalic cœlom, and they

develop into the branchial muscles. No muscles are directly formed from the walls of the branchial portion of the cephalic cœlom, which subsequently retreats from the head.

MANDIBULAR MUSCLES.

Scyllium.—On the formation of the palato-quadrate, in 16 mm. embryos, the mandibular myotome lies outside of and across the palatine process, and then separates into an upper

TEXT-FIG. 7.
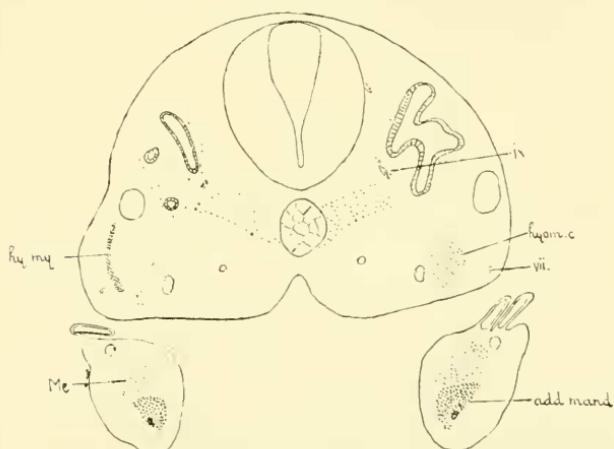
7.

Scyllium, embryo 17 mm., transverse section. The right side of the section is slightly anterior to the left.

levator maxillæ superioris and lower adductor mandibulæ, the process beginning in 20 mm. embryos (Text-fig. 11). The separation of these two muscles by the palato-quadrate is complete, and this is also the case in Acanthias, where, acccording to Marion, the hinder portion of the levator maxillæ superioris—forming a separate first dorsal constrictor—is inserted into the lower jaw. This must consequently be the result of secondary downgrowth. The upper edge of the adductor mandibulæ gains, anteriorly, an additional origin from the suborbital cartilage in 30 mm. embryos (Text-fig. 17), and this anterior portion of the adductor separates, in 40 mm.

embryos, forming the levator labii superioris (or add. β) of
Vetter.   In 45 mm. embryos the add. γ of Vetter is begin-
ning to be delaminated from the outer face of the adductor,
and the hindmost fibres of the adductor have grown down
into the intermandibularis, forming a band similar to that
described in Acanthias by Vetter.

The intermandibularis (Cs_2 of Vetter, C_2mv of Ruge) is
formed from the ventral part of the mandibular cavity,

TEXT-FIG. 8.
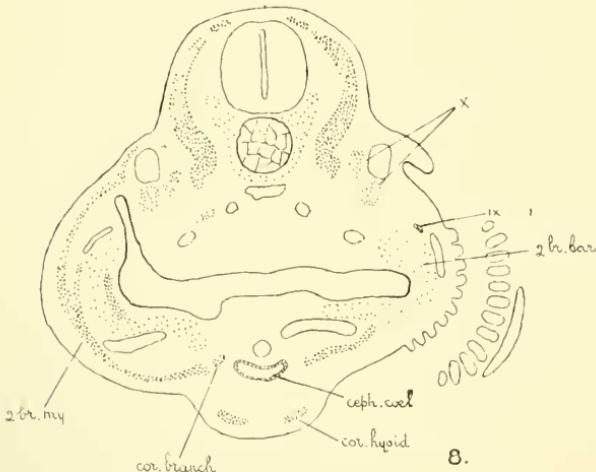

Scyllium, embryo 17 mm., transverse section.

which, as mentioned above, does not meet its fellow in the
mid-ventral line, but passes backwards ventro-median to the
ventral end of the hyoid cavity to open into the front end of
the cephalic cœlom.   It results from this that there is no
developmental stage in which the intermandibularis lies
altogether in front of the interhyoideus.   It gradually extends
backwards, underlying the interhyoideus, so that in 23 mm.
embryos its hinder edge lies posterior to the ventral ends of
the ceratohyals (Text-fig. 12).

The nictating muscles of Scyllium (Ridewood) consist of a
levator palpebræ nictitantis, retractor palpebræ superioris,

and constrictor spiraculi—all innervated by the Vth. Ride-
wood supposed that the first-named was differentiated from the
same tract as the levator maxillæ superioris and that the
second belonged to the same category, whilst the constrictor
spiraculi appeared to belong to a purely dermal system of
muscles.

According to Harman, the musculature of the eyelids of
Mustelus arises " from two original sources—one a superficial
dermal layer, the other a portion of a deeper dermal muscle
layer," the former originating from " a mass which appears

TEXT-FIG. 9.
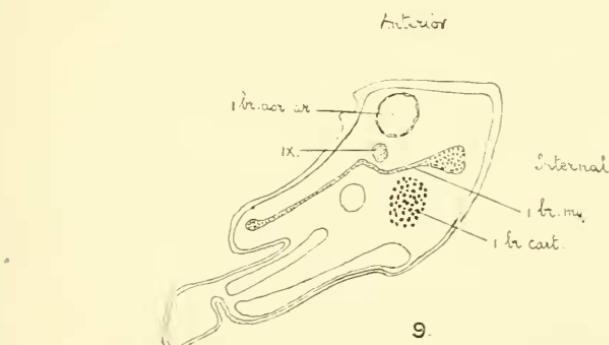
Scyllium, embryo 20 mm., longitudinal horizontal section through
first branchial segment on left side.

first in the region of the branchial bar which is the second
after the spiracle," the latter from a mass which separates
into "a maxillary mass and a spiracular mass." Harman
also stated that " the progressive growth of the spiracle
muscles in the service of the face can be traced to their full
development in the facial muscles of man."

In Scyllium the Anlage of the nictating muscles can be seen
in 30 mm. embryos (Text-figs. 16, 17) as a mass of cells being
proliferated from the outer surface of the upper end of the
levator maxillæ superioris. In 40 mm. embryos the mass
has become partially divided into a deeper and a more
superficial layer—the former is the Anlage of the levator

F. H. EDGEWORTH.
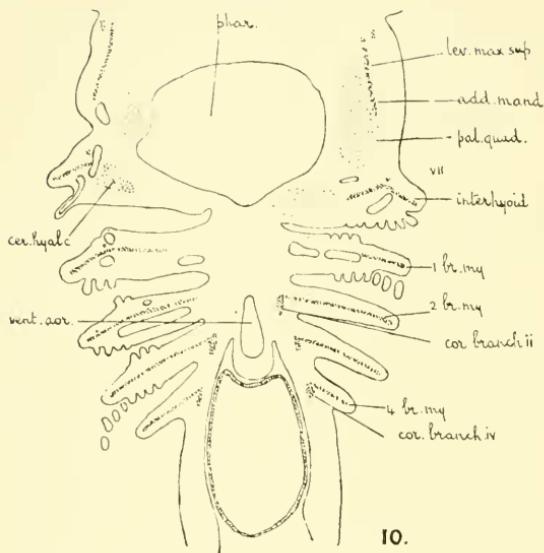
TEXT-FIG. 10.

TEXT-FIG. 11.
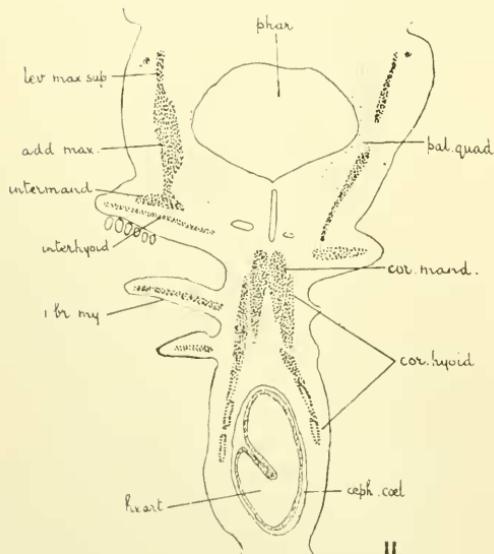
Text-figs. 10 and 11.— Scyllium, embryo 20 mm.   Text-fig. 10
is the more dorsal.

palpebræ nictitantis, the latter that of the retractor palpebræ superioris. In 45 mm. embryos, the latter sends down behind the spiracle an offshoot which develops into the constrictor spiraculi. All these muscles in Scyllium are thus developed from an Anlage budded off from the levator maxillæ superioris. It may be added that the facial muscles of mammals are hyoid in origin, formed from the upgrowing interhyoideus (pp. 221 and 222), and consequently are not homologous with the eyelid muscles of Scyllium.

The myotome of the mandibular segment in Teleostoman embryos lies at first across and outside the palatine process of the quadrate (Text-fig. 23) and then divides into parts above and below this. The division takes place in Acipenser in $7\frac{1}{2}$ mm., in Lepidosteus in $8\frac{1}{2}$ mm., in Amia in $6\frac{1}{2}$ mm., and in Salmo in 5 mm. embryos. The part above the palatine process is the levator maxillæ superioris, the part below the adductor mandibulæ. From the upper end of the levator maxillæ superioris of Lepidosteus, Amia (Text-fig. 28), and Salmo, is given off the dilatator operculi, which extends backwards below the first gill-cleft into the opercular fold, and the remainder forms the levator arcus palatini, which is inserted into the palato-quadrate (Text-fig. 28). In Acipenser the levator maxillæ superioris does not divide into levator arcus palatini and dilatator operculi; it grows backwards, without having had any temporary insertion into the palato-quadrate, and becomes inserted into the hyomandibula, forming the protractor hyomandibularis (Text-figs. 18, 19, 20).

The dilatator operculi is partially inserted into the hyomandibula in Lepidosteus, and wholly in Polypterus, ? species, described by Pollard,[1] but in Polypterus senegalus it passes backwards in the outer wall of the spiracle and is inserted into skin only (Text-figs. 35, 36). The adductor mandibulæ, at first passing from the palato-quadrate to Meckel's cartilage,

[1] Protractor hyomandibularis of Pollard, but not homologous with the protractor hyomandibularis of Acipenser, as he describes a levator maxillæ superioris (i. e. levator arcus palatini), and this is also present in Polypterus senegalus.

TEXT-FIG. 12.

12.
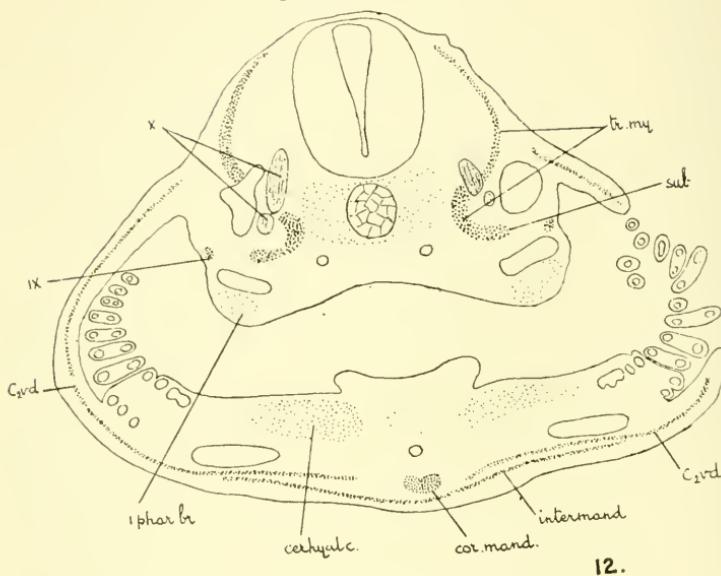
TEXT-FIG. 13

13.
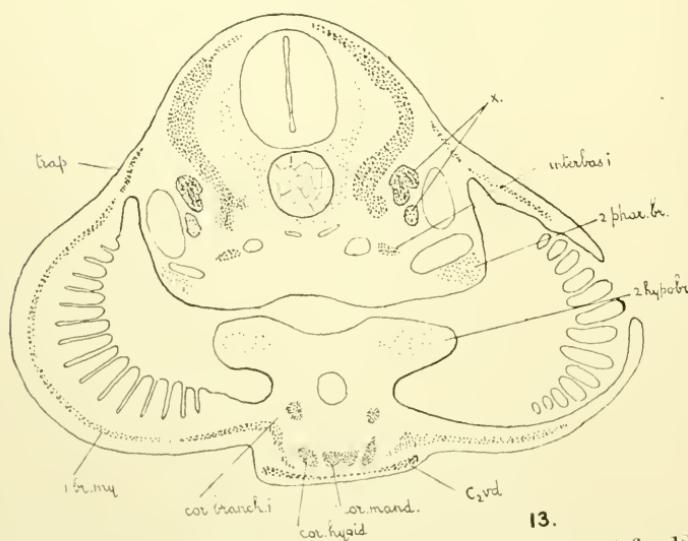
Text-figs. 12 and 13.—Scyllium. embryo 23 mm.   Text-fig. 12
is the more anterior.

undergoes various changes in the specimens examined. In Acipenser embryos up to the length of 11 mm. it remains undivided, but in the adult (Vetter) it has additionally spread up to the skull. In Salmo it additionally spreads backwards to the hyomandibula. In Lepidosteus, Amia (Text-figs. 28, 34), and probably (vide infra) Polypterus, the adductor mandibulæ divides into internal and external portions. In Lepidosteus (Text-figs. 26, 27) the internal portion extends upwards outside the palato-quadrate to gain an additional origin from the cranial wall; whilst the external portion, keeping its original origin, arises from the external surface and upper end of the quadrate outside the insertion of the levator arcus palatini. In Amia[1] the internal portion (in 11 mm. embryos) sends forwards a projection from its upper end which forms the muscle connected with the olfactory chamber (LAP_5 of McMurrich, LMS_4 of Allis); in 14 mm. embryos the remainder of the internal portion extends upwards above the level of the palato-quadrate and divides into three parts ($LAP_{2, 3, 4}$ of McMurrich, $LMS_{2, 1, 3}$ of Allis). The external portion of the adductor additionally extends backwards to the hyomandibula in 9 mm. embryos, and divides into the parts described, as parts of the adductor, by Allis.

In Polypterus, Pollard described the adductor as consisting of three parts, the pterygoid, temporal, and masseter[2]; of

[1] The adult condition of the mandibular muscles of Amia has been described by McMurrich and by Allis. McMurrich stated that they consist of a levator arcus palatini and an adductor mandibulæ, and that the former is divided into five parts—from behind forwards $LAP_{1, 2, 3, 4, 5}$; of these LAP_1 is inserted into the metapterygoid with some of its hindmost fibres into the operculum, $LAP_{2, 3, 4}$ join the adductor, and LAP_5 is in connection with the olfactory chamber. Allis separated LAP_1 into a dilatator operculi and a levator arcus palatini, whilst $LAP_{2, 3, 4, 5}$ he called the second, first, third and fourth divisions of the levator maxillæ superioris. He suggested that LAP_4 and $_5$ (LMS_3 and $_4$) are derived from add. β of Selachians, and that (his) levator arcus palatini and dilatator operculi are the homologue of add. γ of Selachians. From the embryological findings mentioned above it would appear that a new nomenclature for $LAP_{2, 3, 4, 5}$ ($= LMS_{2, 1, 3, 4}$) is needed—in terms of an internal adductor.

[2] Pollard thought that the pterygoid and temporal were the homologue

these the pterygoid and temporal are together the homologue of the internal adductor, and the masseter the homologue of the external adductor, of Lepidosteus and Amia.

Text-fig. 14.
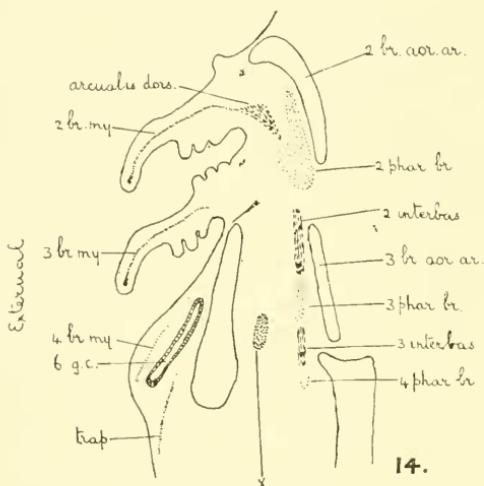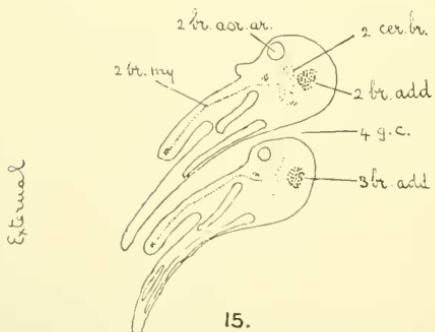
Text-fig. 15.

Text-figs. 14 and 15.—Scyllium, embryo 28 mm., longitudinal horizontal sections. Text-fig. 14 is the more dorsal, through second, third, and fourth branchial segments on left side.

of Add. β of Selachians, but this is not possible. In Text-figs. 35 and 36 I have denoted his " masseter " by the term " external adductor," and his pterygoid and temporal might be called parts of the internal adductor.

The intermandibularis of Teleostoman embryos forms, at first, with its fellow, a transverse muscle attached laterally to Meckel's cartilage (Text-figs. 23, 24, 28).

In Salmo it does not extend backwards, but does so in Acipenser, Lepidosteus, Amia and Polypterus, and partially underlies the fore part of the interhyoideus. In Salmo, Polypterus,[1] and Lepidosteus, it remains single, in Acipenser and Amia it divides into anterior and posterior parts. In

TEXT-FIG. 16.
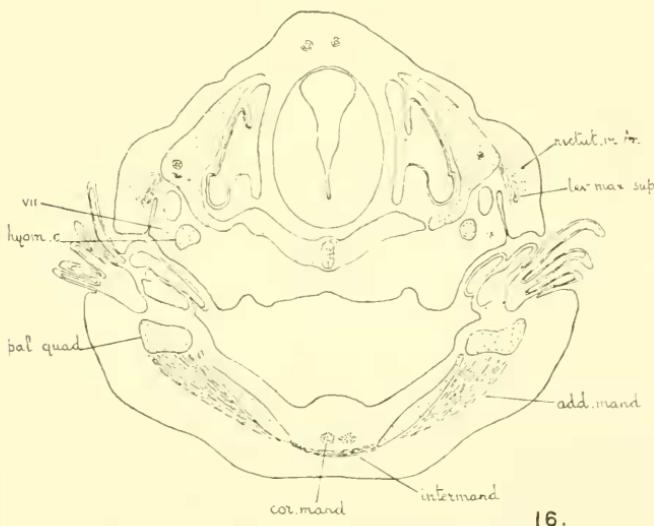
Scyllium, embryo 30 mm., transverse section.

Acipenser the intermandibularis anterior (Cs_6 of Vetter) is attached laterally to Meckel's cartilage, and the intermandibularis posterior (Cs_1 and Cs_2 of Vetter) spreads upwards, laterally, towards the skull.[2] In Amia both intermandibularis anterior[3] and posterior[4] are attached laterally to

[1] Intermaxillaris anterior of Pollard.

[2] All these parts are innervated by the Vth (Allis).

[3] Intermandibularis of Allis.

[4] Superficial or inferior portion of geniohyoid of Allis; the muscle has. however, no genetic relation to the superior portion of the geniohyoid (called in this paper " hyomaxillaris ") which is developed in the hyoid segment.

Meckel's cartilage (the process of separation into anterior and posterior portion beginning in $9\frac{1}{2}$ mm. embryos and being completed in 14 mm. embryos).

In Ceratodus the myotome of the mandibular segment spreads upwards lateral to the Gasserion ganglion (Text-fig. 39), and separates from the lateral half of the intermandibularis between stages 40 and 42 (of Semon). It divides into outer and inner portions—pterygoid[1] and temporal[2]—the former of which, in stage 48 (Text-fig. 46), arises from the trabecular wall, and the latter from the anterior and outer surface of the quadrate. The intermandibularis[3] joins its fellow in a median raphé and becomes attached laterally to Meckel's cartilage ; its posterior edge extending backwards underlies the fore part of the interhyoideus (Text-figs. 41, 45).

In Necturus (Miss Platt) the mesothelium of the mandibular arch (here interpreted as "myotome") divides into an internal part, the temporal (here called, following Drüner, the "pterygoid"), and an external part, the masseter. In Triton the myotome of the mandibular segment also divides into an internal and an external part; the upper end of the internal, pterygoid, part extends up to the side of the skull; the external part, at first arising from the suspensorium only, divides into an outer portion, the masseter, which keeps this origin, and an inner portion, the temporal, which extends up to the auditory capsule.

The intermandibularis of Necturus[4] remains single, its posterior edge underlies the anterior interhyoideus (Text-fig. 55); in Triton the intermandibularis (in larvæ between the lengths of $8\frac{1}{2}$ and 10 mm.) divides into anterior and posterior parts,[5] the latter of which partially underlies the interhyoideus.

---

[1] Pterygoid of Jaquet.

[2] Adductor mandibulæ seu digastricus of Jaquet.

[3] C.mv of Ruge ; mylohyoideus pars anterior of Jaquet.

[4] Mylohyoideus anterior of Mivart and Miss Platt.

[5] Intermaxillaris anterior and posterior of Wiedersheim ; intermandibularis anterior and posterior of Drüner.

The myotome of the mandibular segment of Rana separates
from the lateral half of the intermandibularis in 5 mm.
embryos; it extends backwards in 7 mm. embryos, dividing
into internal and external portions (Text-fig. 58). The myo-
tome thus comes to lie in a nearly horizontal position internal
to the muscles developed in the hyoid segment. The internal
portion develops into the pterygoid muscle, the external into
the temporal, sub-temporal, extra-temporal, and masseter
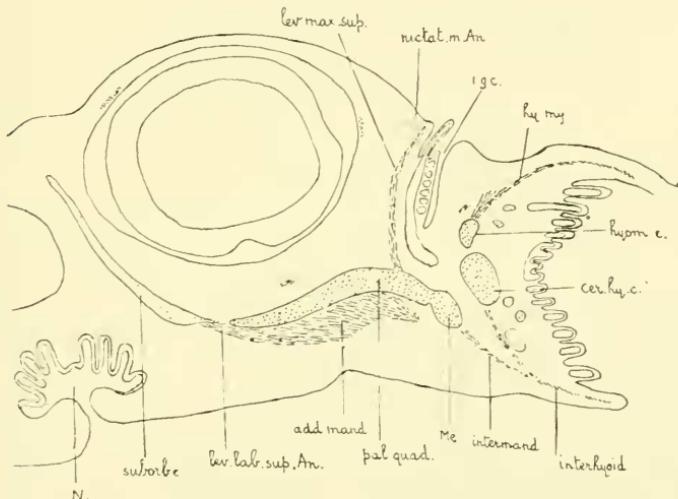
TEXT-FIG. 17.

Scyllium, embryo 30 mm., longitudinal vertical section.

(Text-figs. 59, 60). The masseter and extra-temporal arise
from the internal surface of the processus muscularis of the
palatoquadrate bar. The anterior end of the pterygoid shifts
outwards beneath the anterior ends of the other muscles and is
inserted into the outer end of Meckel's cartilage. The tem-
poral is inserted into the inner end of Meckel's cartilage; the
masseter is inserted into Meckel's cartilage a little distance
from its outer end; the subtemporal is inserted, by two
tendons, into Meckel's cartilage and the superior labial car-
tilage; the extra-temporal divides into two portions, one of

Text-fig. 18.
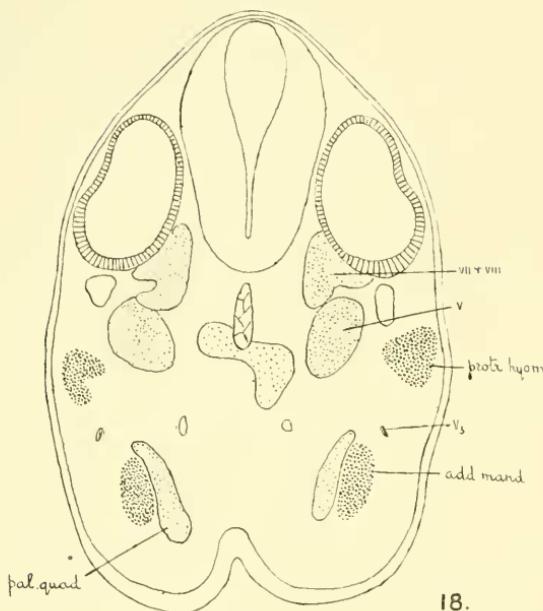
Text-fig. 19.
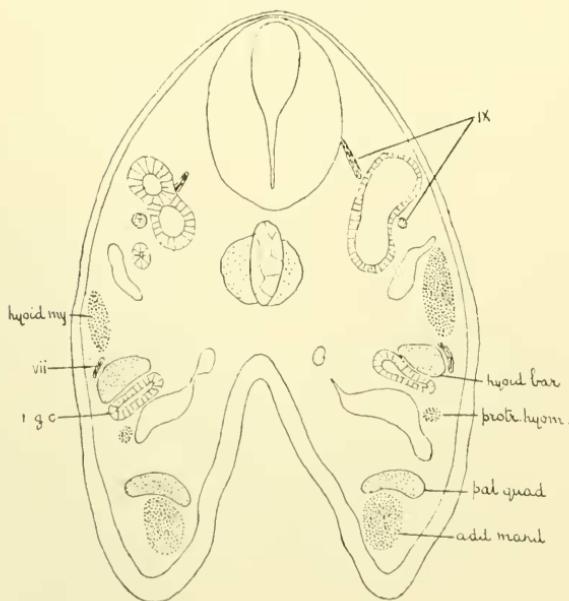
Text-figs. 18 and 19.—Acipenser, embryo 8 mm. Text-fig. 18
is the more anterior.

which joins the temporal (Text-fig. 60) and the other the sub-temporal.

The muscles of Alytes, Bufo lentiginosus, and Pelo-bates[1] are similar to those of Rana (Text-fig. 63), except that the extra-temporal is inserted only into the superior labial cartilage.

The Anlage of the levator bulbi is given off from the upper surface of the hinder part of the temporal in 9 mm. larvæ; its outer end becomes inserted into the skin and upper edge of the palato-quadrate bar; it remains relatively undeveloped until late in metamorphosis. On the development of the lower eyelid a slip is separated from the levator bulbi, forming the depressor palpebræ inferioris.

At metamorphosis, on the atrophy of the superior labial cartilage the sub-temporal and extra-temporal fuse with the temporal, and the muscles become more vertical in position on the rotation of the palato-quadrate bar.

The Anlage of the intermandibularis of Rana divides in 7 mm. embryos into three parts—the submentalis, the man-dibulo-labialis, and the submaxillaris. The submentalis develops later than the other two muscles; in 12 mm. embryos it forms a mass of small round cells lying beneath and extending backwards from the inferior labial cartilages, and at the beginning of metamorphosis forms a layer of trans-versely directed muscle-fibres connecting together the infe-rior surfaces of the inferior labial cartilages (Text-fig. 60). The mandibulo-labialis, arising from the inner aspect of the transversely directed Meckel's cartilage, passes down external to the genio-hyoid and is partially inserted into skin, partially interlaces with the muscle of the opposite side (Text-fig. 60).

The submaxillaris arises from the under surface of Meckel's cartilage. The conditions in larvæ of Bufo lentiginosus

[1] This account differs from that of Schultze, in that the subtemporal is stated to be inserted into Meckel's cartilage as well as into the superior labial cartilage, and in the description of an extra-temporal. The results were obtained from serial sections of larvæ, 10, 13, 22, and 30 mm. long.

TEXT-FIG. 20.
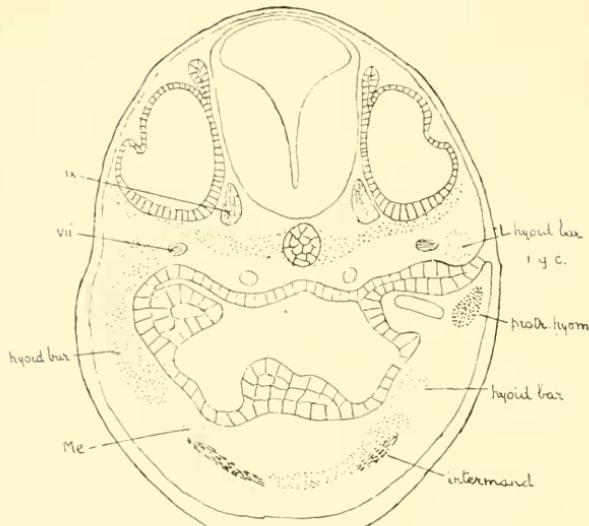
20.

TEXT-FIG. 21.
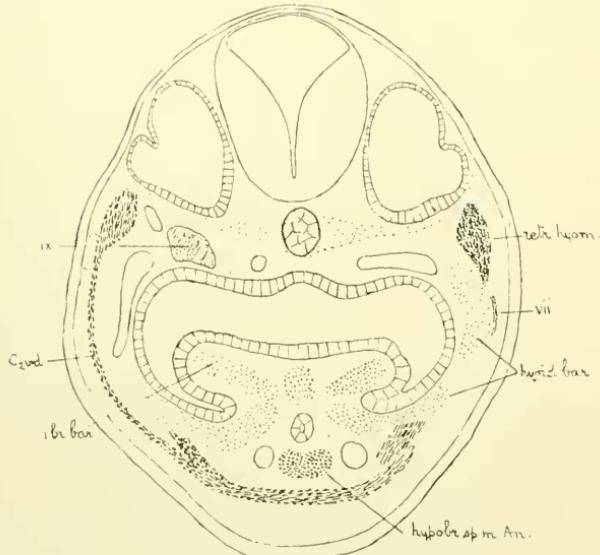
21.

Text-figs. 20 and 21.—Acipenser, embryo 8½ mm. Text-fig. 20
is the more anterior. The right side of the sections is slightly
anterior to the left.

are similar to those of Rana ; in Alytes the submaxillaris arises, like the mandibulo-labialis, from the inner aspect of Meckel's cartilage, so that the two muscles are much more continuous than is the case in Rana, Bufo, and Pelobates. The condition in 10 mm. larvæ of Pelobates is similar to that of 12 mm. larvæ of Rana ; in 13 mm. larvæ the mandibulo-labialis has spread additionally into the upper lip, the condition described by Schultze. He states that the submentalis is attached to the inner aspect of Meckel's cartilage, but up to the stage of 30 mm. it is attached, as in Rana, Bufo, and Alytes, to the inferior labial cartilages, as a very minute transverse muscle.

At metamorphosis in Rana, the attachment to the skin of the mandibulo-labialis is lost, and the muscle forms one sheet with the submaxillaris.[1]

Observations on the development of the mandibular muscles have been made by Reuter in pig-embryos, and in regard to the tensor tympani by Futamura in human embryos. Reuter stated that the mandibular muscles are first visible in pig embryos measuring 16 mm. in " Nacken-Steisslänge "[2] in the form of an inverted **Y**, the two limbs of which lie on either side of the lower jaw. The temporal develops from the upper limb, the masseter from the lower external limb, and the two pterygoids from the lower internal limb. No mention is made of the tensor tympani or the palatine muscles. According to Futamura the tensor tympani and tensor veli palatini form a " ganz einheitlichen Muskel " in human embryos of seven weeks. This Anlage and the levator veli palatini are developed about the branches of the palatine nerves from a " Muskelblastemgewebe " which " deutlichen Zusammenhang mit dem tiefen Teil der Platys-maanlage erkennen lässt." " Die Nervenäste für diese

[1] Submaxillaris of Ecker and Gaup.

[2] This stage is an advanced one, as the figures show that the ossification of the lower jaw has begun. The Anlage of the mandibular muscles was quite evident in a pig embryo of 8 mm. crown-rump measurement, from which Text-fig. 98 was taken.

Muskeln lassen sich leicht vom Facialis hervorfolgen."[1]
He also states that in pig embryos the levator veli palatini
and M. uvulæ develop as in man from "Gewebe des
Platysma colli das von der vorderen Seite des Oberkiefer-
fortsatzes nach seiner medialen Seite zieht."

In 2 mm. embryos of the rabbit the cells which will form
the myotome of the mandibular segment cannot be differen-
tiated from the other cells occupying the segment. In
3 mm. embryos (Text-fig. 76) the myotome is visible, and the
walls of the mandibular section of the cephalic cœlom are
beginning to come together, forming the intermandibularis.
The myotome separates from the lateral edge of the inter-
mandibularis in 7 mm. embryos. In 13 mm. embryos it has
partially separated into external and internal portions, which
form the two limbs of a Λ-shaped mass, the apex of which
lies just below the Gasserian ganglion (Text-figs. 94, 95); the
external portion is the Anlage of the temporal masseter and
external pterygoid muscles; it extends up to the skull in
16 mm. embryos, the external pterygoid is cut off from the
internal surface of the lower end of the temporal. The
internal portion separates into internal pterygoid and tensor
tympani. The intermandibularis forms the mylohyoid of the
adult; it is covered over, in 10 mm. embryos, by the forward
growing interhyoideus.

The Homologies of the Mandibular Muscles.—Com-
parison of the various ways in which the myotome of the mandi-
bular segment develops shows that they may be reduced to two
types : (1) That in which the myotome does not divide into
upper and lower portions—Ceratodus, Necturus, Triton, Rana,
Alytes, Bufo lentiginosus, Pelobates, Lepus. (2) That in
which the myotome divides into portions above and below
the palato-quadrate, into levator maxillæ superioris and
adductor mandibulæ—Scyllium, Acipenser, Lepidosteus, Amia,
Salmo, Sauropsida.

Drüner supposed that a portion homologous with the

[1] Beevor and Horsley showed, however, that no movement of the palate
is produced in the monkey on intra-cranial stimulation of the VIIth.

levator maxillæ superioris of Selachians disappears in Amphibia.[1] There is, however, no trace of this in the ontogeny of Amphibia. According to Gaupp the pterygoid process of Amphibia presents features which lead to the
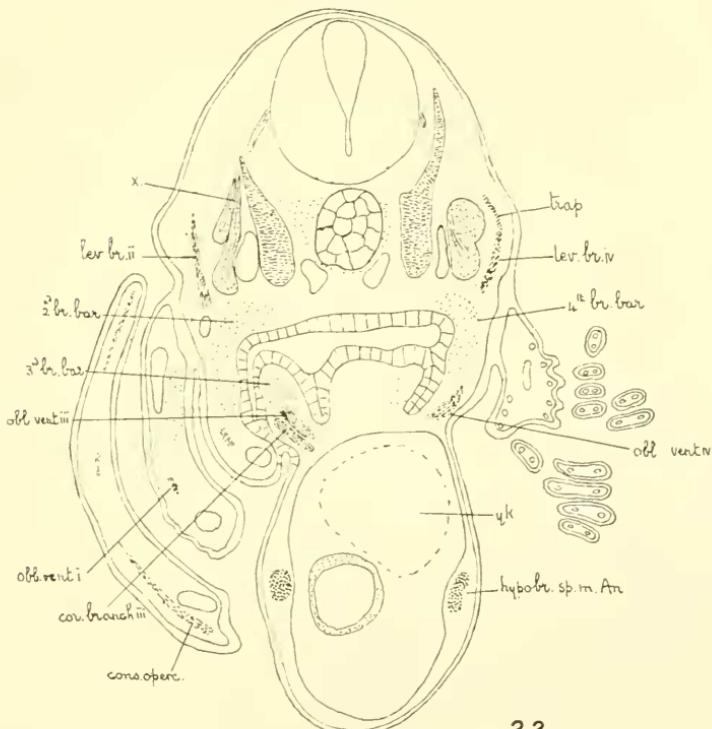
TEXT-FIG. 22.

Acipenser, embryo $8\frac{1}{2}$ mm. The left side of the section is slightly anterior to the right.

suggestion that it is in process of "Rückbildung." If this be so, and if the pterygoid process of Amphibia be homologous with that of Selachians—a matter which Gaupp says

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[1] The levator maxillæ superioris "ist wohl mit der Verwandlung der Streptostylie in die Monimostylie der Urodela verloren gegangen."

is not certain—it might be supposed that a muscle strip which formerly divided into upper and lower portions now by some atavistic process no longer does so. On the other hand, the fact that, in all the animals of the second class, the myotome, undivided, lies at first across and unattached to the palato-quadrate, i.e. shows a condition which is the permanent one in Amphibia and Ceratodus, suggests that the con-

TEXT-FIG. 22A.
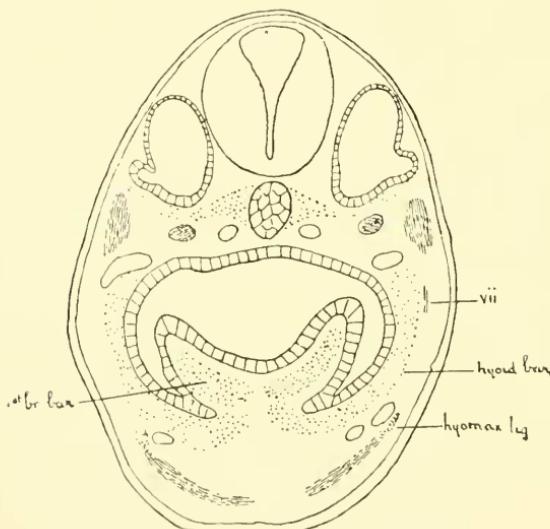
Acipenser, embryo 9 mm.

dition in Amphibia, Ceratodus, and Mammalia is the primary one, and that the one present in Selachii, Teleostomi, and Sauropsida is a secondary one. It would follow that the palatine or pterygoid process of the quadrate was not primarily a process for attachment of muscles nor an upper jaw.

Fürbringer divided Vertebrates into two classes with regard to the connection of the quadrate with the skull— those with movable quadrates (streptostylic), and those with immovable quadrates (monimostylic). The latter condition,

he thought, was secondary to the first. " Die Monimostylie allgemein von der Streptostylie ableitet."

The development of the mandibular muscles in the Sauropsida suggests that in them there are two streptostylic conditions—a primary streptostylic pterygo-quadrate in birds, and a secondary streptostylic quadrate in Lacerta vera,
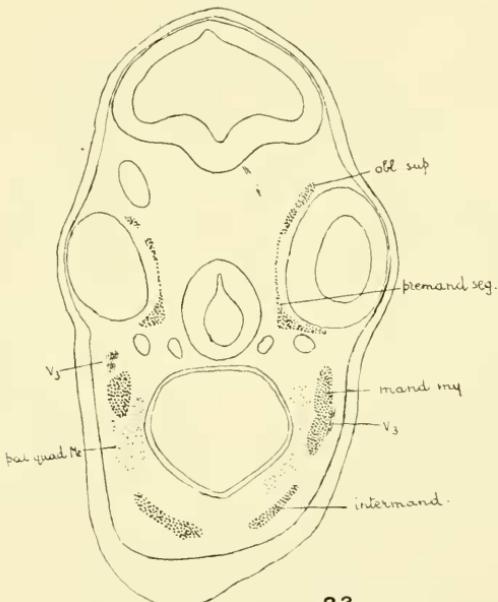
TEXT-FIG. 23.

Lepidosteus, embryo 8 mm., transverse section.

Rhiptoglossa, and Ophidia, and that the monimostylic condition of Chelonia, Crocodilia, and Rhyncocephalia was developed—and probably independently—from a primitive streptostylic pterygo-quadrate which has been preserved in Birds (loc. cit.).

The development of the mandibular muscles in Amphibia and Ceratodus affords no evidence that the monimostylic condition there present has been derived from a streptostylic one, and a fixed quadrate would appear to be a necessary

correlative of an undivided mandibular myotome, to form a point d'appui for the lower jaw.

It would follow that the streptostylic condition present in Selachians, Teleostomi, and Sauropsidan embryos is one which developed in correlation with a division of the myotome into upper and lower parts, inserted into and arising from the palatine process of the quadrate.

TEXT-FIG. 24.
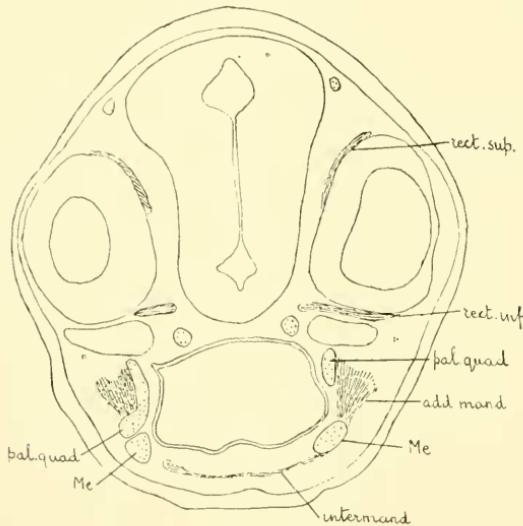
24.

Lepidosteus, embryo 12 mm., transverse section.

In Ceratodus, Amphibia, and Lepus, where the mandibular myotome does not become divided into upper and lower parts, it separates into internal and external portions. In the Anuran larvæ the outer division divides into parts, some of which have a temporary insertion into the superior labial cartilage, and the whole myotome assumes a nearly horizontal position in correlation with that of the palato-quadrate bar; at metamorphosis both bar and muscles rotate into a more vertical position. In the rabbit the inner division separates into the internal pterygoid and the tensor tympani

muscles, the outer division into the temporal, masseter, and external pterygoid.

Secondary changes take place in the levator maxillæ superioris and adductor mandibulæ in all the animals investigated; no one preserves them as such. In Scyllium the

TEXT-FIG. 25.
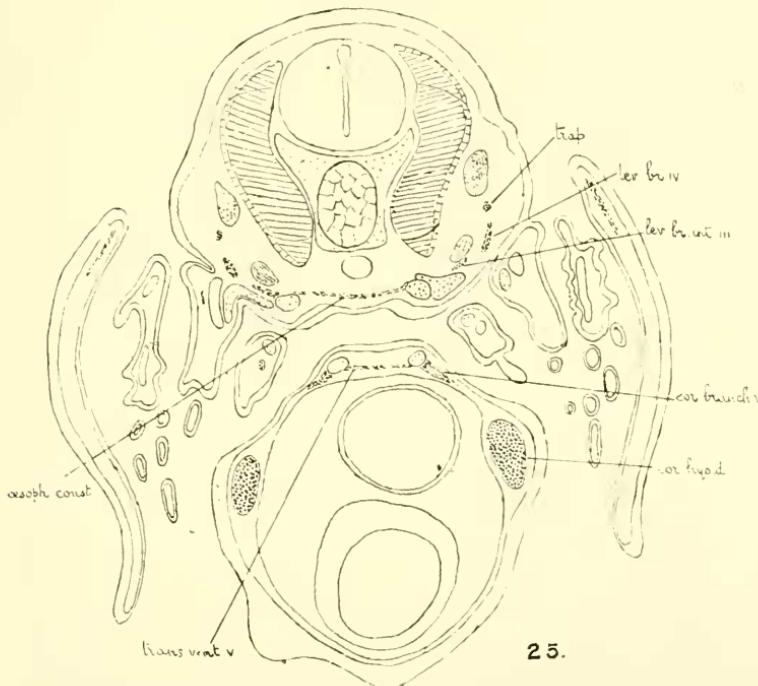
Lepidosteus. embryo 14 mm., transverse section.

Anlage of the nictating muscles is proliferated from the levator maxillæ superioris, and add. β and add. γ are separated from the adductor. In Teleostomi the levator maxillæ superioris either forms a protractor hyomandibularis or divides into a dilatator operaculi and levator arcus palatini; and the adductor may either remain single as in Salmo, or divide into external and internal portions, of which either the internal (Lepidosteus), or both (Amia, Polypterus), or ? the

TEXT-FIG. 26.

obl. sub

obl. inf.

add. mand. int.

add. mand. ext.

pal. pr. of quad.

quad.

Mc.

Mc.

26.

intermand.

TEXT-FIG. 27.

iii.

rect. ext.

lev. arc. pal.

add. mand. ext.

interhyal.

pal. quad.

hyomax. lig.

obl. inf. i.

cer. hyal. c.

hyohyoid. inf.

hyohyoid. sup.

cor. hyoid.
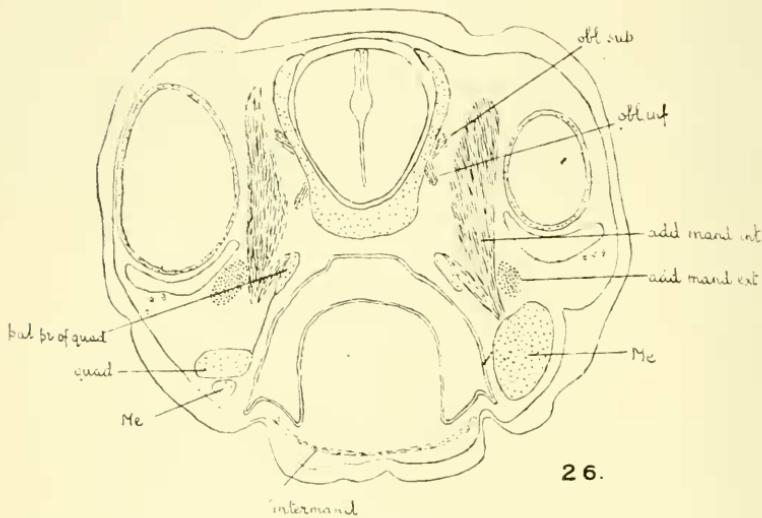
27.
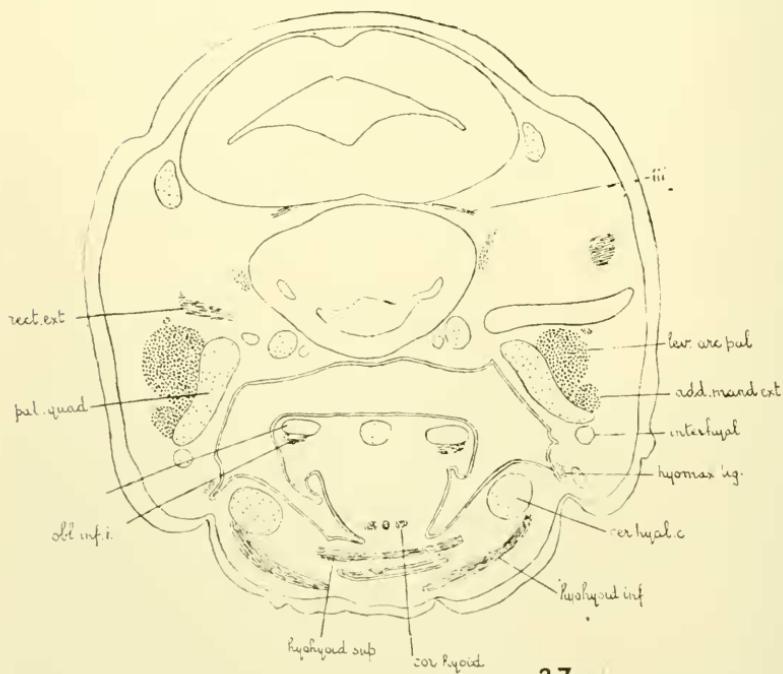
Text-figs. 26 and 27.—Lepidosteus, embryo 19 mm. Text-fig. 26
is the more anterior.

external (Acipenser), grows up to the skull. In Sauropsidan embryos the depressor palpebræ inferioris is given off from the anterior margin of the levator maxillæ superioris, which becomes inserted into the palato-quadrate—this is preserved in birds, whereas in reptiles various changes, modifications

TEXT-FIG. 28.
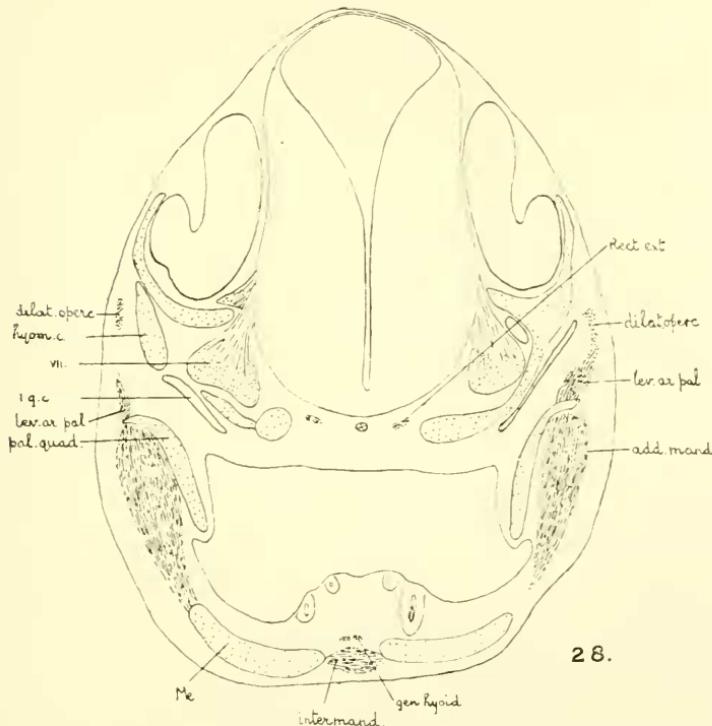
Text-figs. 28-33.—Amia, embryo 8½ mm. Text-fig. 28 is the most anterior.

or atrophy, occur; and the adductor mandibulæ divides into external and internal portions, of which the former grows up to the skull, whilst the primitive origin of the latter was probably to the palato-quadrate and the hind end of the palato-pterygoid bar—this is preserved in Chelonia, but is variously modified in other groups (loc. cit.).

A comparison of the various forms of the intermandibularis

shows that its primitive condition is that of a transverse
sheet passing from one ramus of the lower jaw to the other.
This exists only in Salmo. In Necterus, Triton, Ceratodus,
Scyllium, Acanthias, Polypterus, Lepidosteus, and Amia
it extends backwards, underlying the fore part of the inter-

TEXT-FIG. 29.
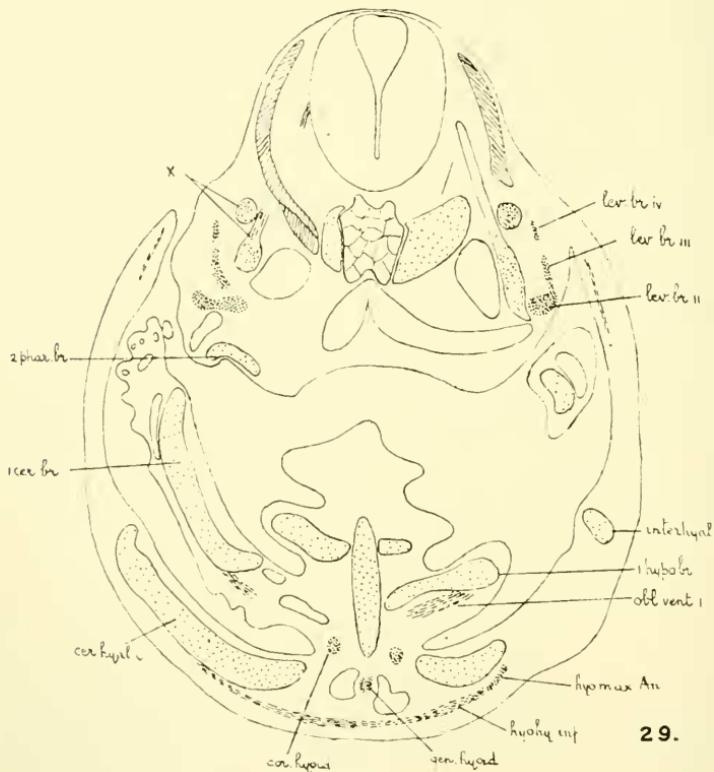
hyoideus, and in Amia and Triton it divides into anterior
and posterior portions. In Anuran larvæ it divides into
submentalis, mandibulo-labialis and submaxillaris, of which
the first has a special relationship to the inferior labial
cartilages. In Sauropsida it forms a continuous sheet with
the interhyoideus and C_2vd. In Lepus it is overlapped by
the forward-growing interhyoideus.

The intermandibularis, in correlation with its development in the mandibular segment, is usually innervated by the Vth cranial nerve. Vetter, however, found that in Scyllium and Prionodon the portion immediately behind the symphysis of the jaws was innervated by the Vth, and the greater portion

TEXT-FIG. 30.

30.
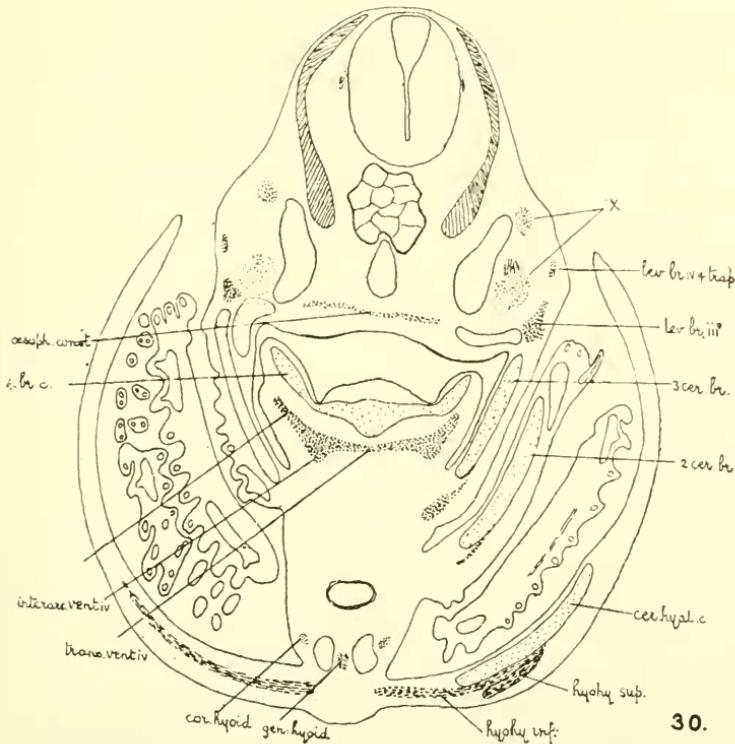
of the muscle by the VIIth, and that in Acanthias, Heptanchus, and Scymnus the whole of the muscle was innervated by the VIIth. He concluded that in the former the greater part, and in the latter the whole, of the intermandibularis (Csv_1) had disappeared, and had been replaced by the interhyoideus (Csv_2), which had gained a secondary insertion into the lower jaw. But this opinion, which was founded on adult

anatomy only, is at variance with the phenomena of development; both in Scyllium and Acanthias a well-marked intermandibularis is formed in the mandibular segment, and spreads back below the interhyoideus and fusing with it behind the hyoid bar. Its partial or total innervation by the VIIth must consequently be a secondary phenomenon.

TEXT-FIG. 31.
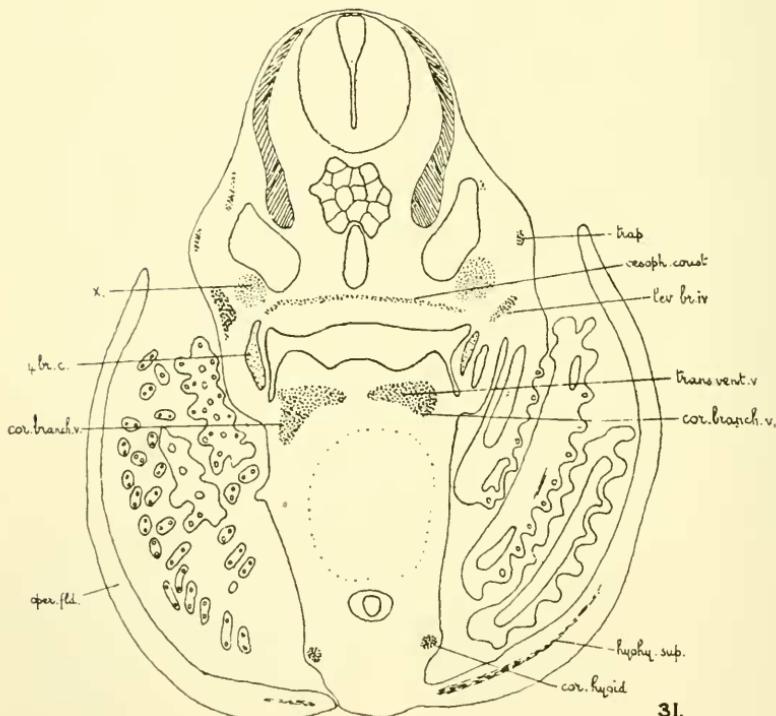
The intermandibularis of Ceratodus is also innervated by the VIIth (Ruge), and its hinder part in Triton (Drüner).

Ruge held that what is here called the intermandibularis is a facial muscle, and that its innervation from the Vth is secondary, but in Ceratodus, as in all the vertebrates examined, it is developed in the mandibular segment. Ruge's theory was based on the idea that " Es liegt auch nicht der geringste

TEXT-FIG. 32.

trap
x.
oesoph const
lev. br v
cor. branch. v.
cor branch. v.
cor hyoid
hyohy. sup.

32.

TEXT-FIG. 33.

tr my o
tr my r.
retr au. br
dilat lary
oesoph cons
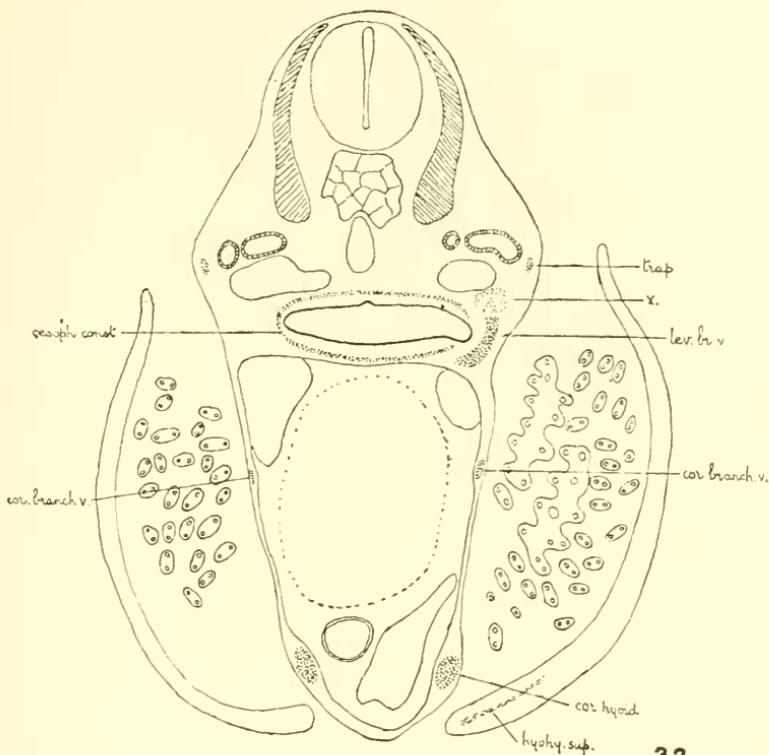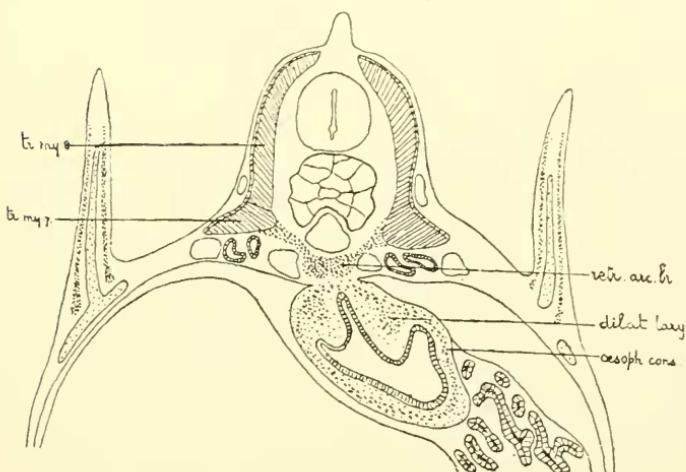
33.

Grund vor um an der Ursprunglichkeit der Einrichtungen bei
den Notidaniden zu zweifeln." Study of the comparative
embryology of the cranial muscles, however, leads to consider-
able doubt on this matter.

HYOID MUSCLES.

In Scyllium the ventral end of the hyoid myotome becomes
continuous with the lateral edge of the future interhyoideus
in 14 mm. embryos. In 16 mm. embryos the formation of
the hyoid bar begins by aggregation of the mesoblast cells,
forming a pro-cartilaginous tract lateral to the alimentary
canal, and the myotome is at first partly continuous with the
interhyoideus, partly inserted into the upper end of the bar
(Text-figs. 5 and 6), forming a levator hyoidei. In 17 mm.
embryos the hyoid bar extends upwards towards the auditory
capsule (Text-fig. 7), partly covered by the myotome, which is
inserted into its lateral surface (C_2hd of Ruge). It is only
later, in embryos between the lengths of 23 and 30 mm., that
the hyoid bar separates into ceratohyal and hyomandibula, as
in Acanthias (Gaupp). The continuity of the myotome and
the interhyoideus becomes lost, and the lateral edge of the
latter is inserted into the ceratohyal. In 23 mm. embryos
(Text-figs. 12, 13, cf. Text-figs. 10 and 11) backward extension
of the myotome and interhyoideus takes place, so that a con-
tinuous dorso-ventral sheet (C_2vd of Ruge) is formed behind
the hyoid bar. Later on, in 40 mm. embryos, the myotome
extends forwards, completely covering the hyomandibular
cartilage, and its anterior edge is inserted into the quadrate.

In the Teleostomi the relations of the fore part of the
hyoid myotome (retractor or adductor mandibulæ) to the
hyomandibular cartilage are different from those existing in
Selachii. The retractor of Acipenser is inserted into its
hinder edge, and of Polypterus into its inner surface, and the
adductor of Lepidosteus, Amia, and Salmo is inserted into
its inner surface. Further, the VIIth nerve (hyoid branch
of VIIth in Polypterus) winds round the cartilage in

Acipenser and Polypterus, pierces it in Lepidosteus, Amia, and Salmo.

The development is not yet known in Polypterus. In the first stages, hitherto described, of Acipenser ruthenus (Parker), Lepidosteus (Parker), and Salmo trutta (Stöhr), the hyomandibula is stated to abut against the auditory capsule. Rutherford[1] states that in the brown trout a downgrowth of no great size, from the periotic capsule at the edge

TEXT-FIG. 34.
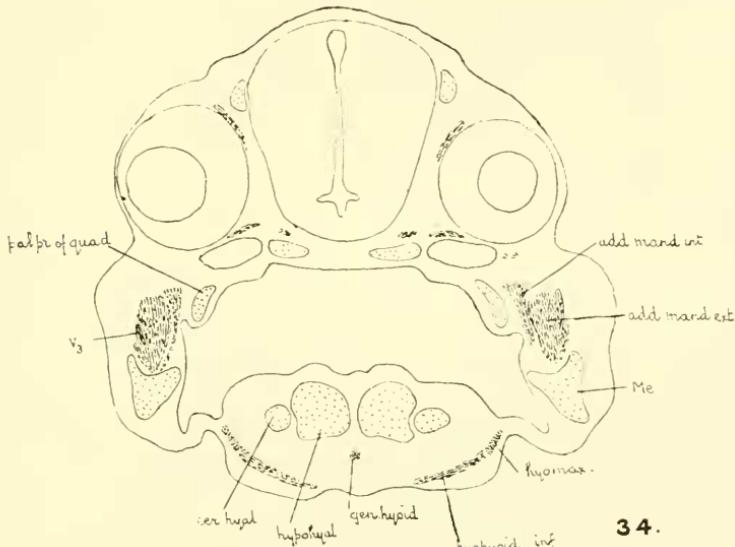
Amia, embryo 10 mm., transverse section.

of the fenestra ovalis, joins with the symplecticum in front of the VIIth nerve, and finally unites with the primitive hyomandibula.

In 8 mm. embryos of Acipenser the hyoid bar, in a procartilaginous condition and unsegmented, does not extend up to the auditory capsule. The VIIth nerve passes over the upper end of the bar, and then downwards outside it (Textfig. 19). In 8½ mm. embryos the hyoid bar extends up towards

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[1] The paper is as yet only published in abstract.

TEXT-FIG. 35.

35.
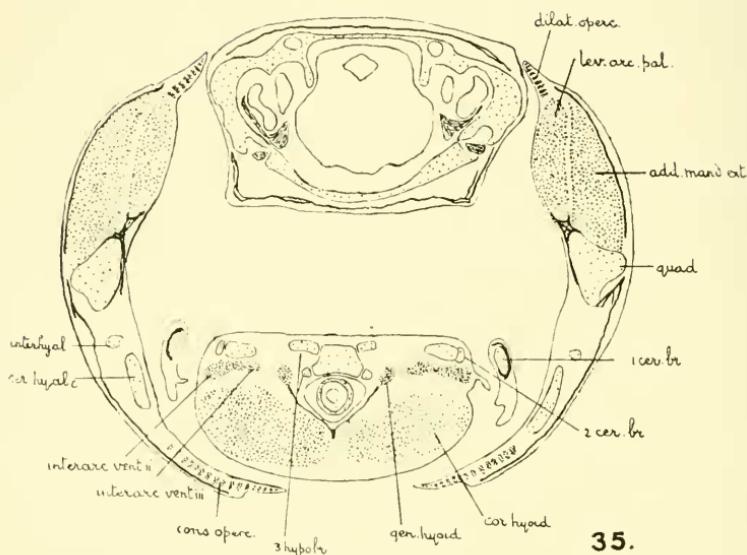
TEXT-FIG. 36.

36.
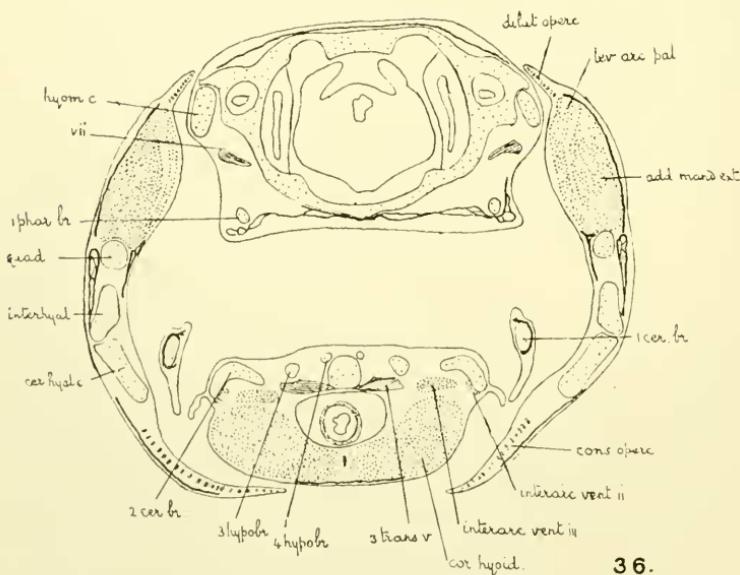
Text-figs. 35–37.—Polypterus, larva 7½ cm.   Text-fig. 35 is the
most anterior.

the auditory capsule and in front of, and outside, the VIIth nerve, which now winds round it (Text-figs. 20 and 21). The hyo-mandibular cartilage is formed in part from the upper portion of the bar present in 8 mm. embryos, and in part from the upward extension. The hyoid muscles in 8 mm. embryos consist of a hyoid myotome, the anterior part of which is inserted into the upper end of the hyoid bar (Text-

TEXT-FIG. 37.
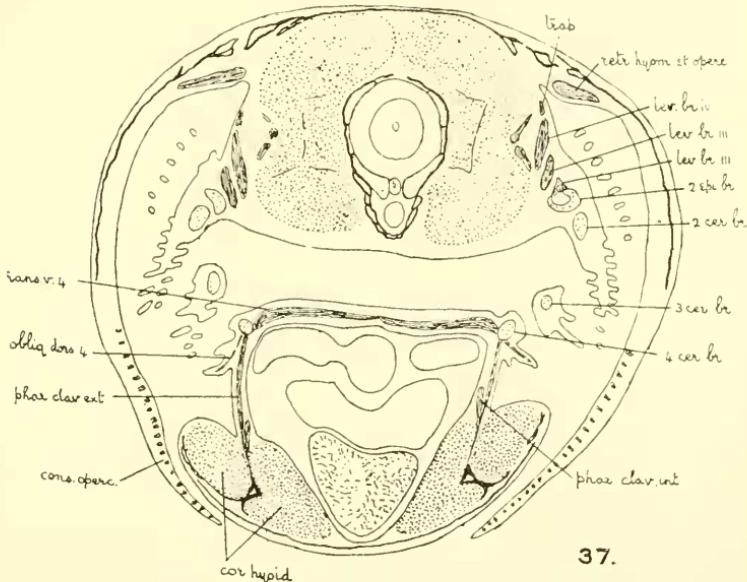
fig. 19), forming a levator hyoidei, and the posterior part of which forms a dorso-ventral sheet—homologous with C_2vd of Selachians—continuous with the posterior part of the inter-hyoideus (Text-fig. 21), whilst the anterior part of the inter-hyoideus is inserted laterally into the hyoid bar.

The sequence of events in the other Teleostomi examined is similar to that occurring in Acipenser, the upgrowth of the hyoid bar to the auditory capsule taking place in 8 mm. embryos of Lepidosteus, $6\frac{1}{2}$ mm. embryos of Amia, and $5\frac{1}{2}$ mm. embryos of Salmo fario. In no case was any downgrowth

from the periotic capsule found. In Lepidosteus, Amia, and
Salmo, the VIIth nerve, at first winding round the hyoid
bar, subsequently pierces the hyomandibula owing to chon-
drification spreading round it; the more primitive condition
is preserved in Acipenser and Polypterus.

The adult condition of the hyoid muscles in these Teleostomi
is not quite uniform. In all the dorso-ventral sheet C_2vd
divides into dorsal and ventral portions. In Polypterus the
anterior and posterior portions of the myotome do not separate
from each other, but form one muscle, the retractor hyomandi-
bularis et opercularis. In the others separation takes place;
the anterior part, i. e. the original levator hyoidei, forms a
retractor hyomandibularis in Acipenser, and an adductor
hyomandibularis in Lepidosteus, Amia, and Salmo. The
posterior part, i. e. the upper part of C_2vd, forms a M.
opercularis in Acipenser and Lepidosteus, an adductor and
levator operculi in Amia and Salmo. In $9\frac{1}{2}$ mm. embryos of
Salmo the adductor mandibularis additionally spreads forwards,
forming the adductor arcus palatini.

The fore part of the interhyoideus of Acipenser forms the
hyoideus inferior (Cs_5 of Vetter), the hinder part, i.e. the
lower part of C_2vd, forms a constrictor operculi (Cs_3 and Cs_4
of Vetter). In Polypterus the condition is similar.[1] In Lepi-
dosteus, Amia, and Salmo, the fore part forms the hyoideus
inferior; the hinder part becomes attached laterally to the
hyoid bar (only partially so in Lepidosteus), and forms the
hyoideus superior. The median raphé of these muscles is
preserved in Acipenser, Lepidosteus, and Polypterus; in
Salmo and Amia it is lost, and the hyoideus inferior becomes
attached to the hypohyals of the same and opposite side.

In $8\frac{1}{2}$ mm. embryos of Amia the Anlage of the hyomaxillaris[2]
muscle becomes separated from the upper edge of the hyo-
hyoideus inferior (Text-fig. 29); it grows forward to Meckel's

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[1] Intermaxillaris posterior and mantle muscle of Pollard.

[2] Superior deeper portion of the genio-hyoid of Allis. A different
terminology is used in this paper, as the word "genio-hyoid" is generally
used to denote the anterior element of the hypobranchial spinal muscles.

TEXT-FIG. 38.
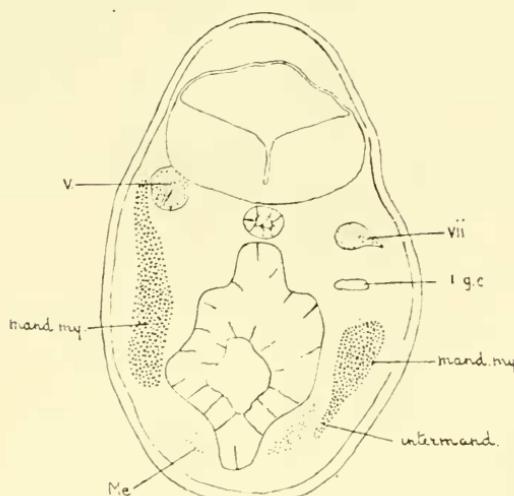
38.

TEXT-FIG. 39.
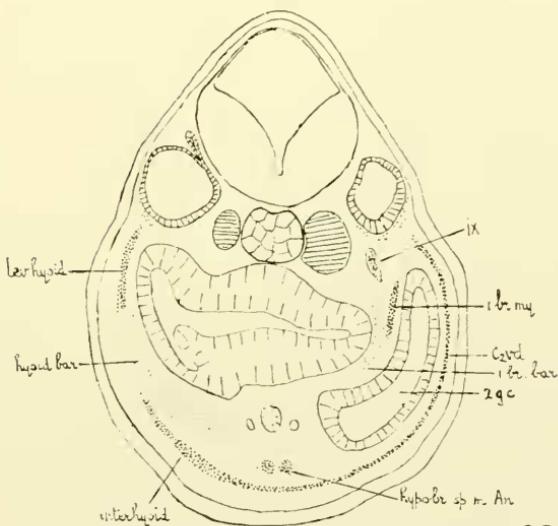
39.

Text-figs. 38 and 39.—Ceratodus, embryo stage 40; transverse sections.   Text-fig. 38 is the more anterior; the left side of the sections is slightly anterior to the right.

cartilage dorsal to the intermandibularis posterior.   A similar
muscle is formed in Salmo ; it grows forward ventral to the
inter-mandibularis.   In $9\frac{1}{2}$ mm. embryos of Lepidosteus and
9 mm. embryos of Acipenser (Text-fig. 22 A) a similar Anlage
is formed from the dorsal edge of the hyoideus inferior or Cs_5
and develops into the hyomaxillaris ligament.[1] In Polypterus,
? species, Pollard described, but did not name, a small muscle
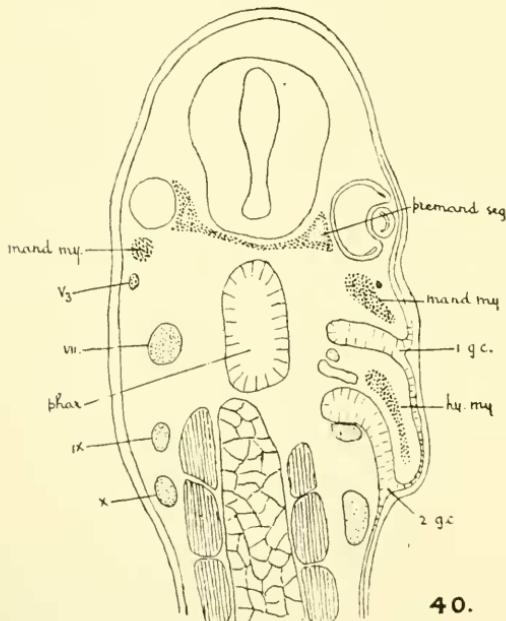
TEXT-FIG. 40.

Text-fig. 40.—Ceratodus, stage 40, longitudinal horizontal section.

" at the angle of the jaw in the substance of the ligament
which binds the hyomandibula quadrate and stylohyal,"
innervated by the opercular branch of the hyoid branch of
the VIIth.   In Polypterus senegalus only a ligament is
present.

In Ceratodus, between the stages of 38 and 40, the hyoid
myotome and interhyoideus spread backward in the opercular

[1] Mandibulo-hyoid ligament of van Wijhe.

fold (Text-fig. 40), and form in the latter stage (Text-fig. 38) anteriorly a levator hyoidei inserted into the upper end of the hyoid bar, and an interhyoideus, and posteriorly a continuous ventro-dorsal sheet C_2vd in the operculum. In stage 42 the Anlage of the hyomaxillaris ligament is cut off from the upper edge of the interhyoideus and spreads forwards to the hind end of Meckel's cartilage (Text-fig. 41). In stage 42 (Text-fig. 41) the hyoid bar extends upwards and inwards towards the under surface of the pro-cartilaginous tract connecting the parachordal plate with the auditory capsule, forming the hyomandibula, the original hyoid bar forming the ceratohyal and hypohyal.

The upper part of the originally pro-cartilaginous hyomandibula chondrifies; the lower forms a fibrous tract connecting its outer end with the upper end of the ceratohyal (Text-fig. 50). In stage 48 a downgrowth occurs from the outer edge of the auditory capsule, external to the hyomandibular branch of the VIIth (Text-fig. 47), and becomes separated, forming a cartilage abutting against the outer end of the hyomandibula (Text-fig. 50), and a second more dorsally situated piece is subsequently cut off from the auditory capsule (Text-fig. 50).[1] The insertion of the levator hyoidei into the upper end of the ceratohyal is preserved in the oldest embryo examined, but is not present in the adult (Ruge) ; it is, however, retained in Protopterus (vide description by Ruge).

In Necturus Miss Platt stated that the "hyoid mesothelial tissue" (here interpreted as "myotome") divided into a dorsal digastricus, which "is ultimately connected with the posterior extremity of the mandibular bar by a long tendon"

[1] This description of the hyomandibula coincides with and amplifies that of K. Fürbringer. The cartilage (or cartilages) cut off from the auditory capsule is probably, from its relation to the hyomandibular branch of the VIIth, that described by Huxley, Ridewood, Ruge, and Sewertzoff as the "hyomandibula." From the descriptions given it would appear probable that no part of a true hyomandibula is preserved in the adult, and that (vide Ridewood) the cartilages cut off from the auditory capsule are variable.

TEXT-FIG. 41.

41.
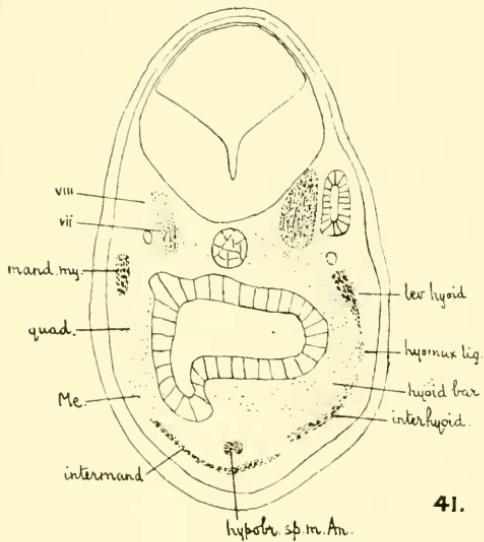
TEXT-FIG. 42.

42.
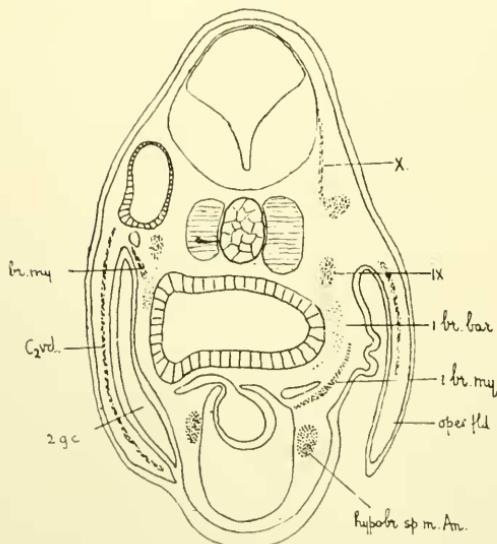
Text-figs. 41-43.—Ceratodus, embryo stage 42; transverse sections. Text-fig. 41 is the most anterior; the left side of the sections is slightly anterior to the right side.

and a ventral ceratohyoidens externus. Examination of sections of $14\frac{1}{2}$ mm. embryos shows that there is a stage in which the future digastricus (the "cephalo-dorso-mandibularis" of Drüner) forms a levator hyoidei, inserted into the upper end of the hyoid bar, whilst below the cerato-hyoidens externus the Anlage of the hyomaxillaris ligament is formed (Text-fig. 55).

TEXT-FIG. 43.

43.
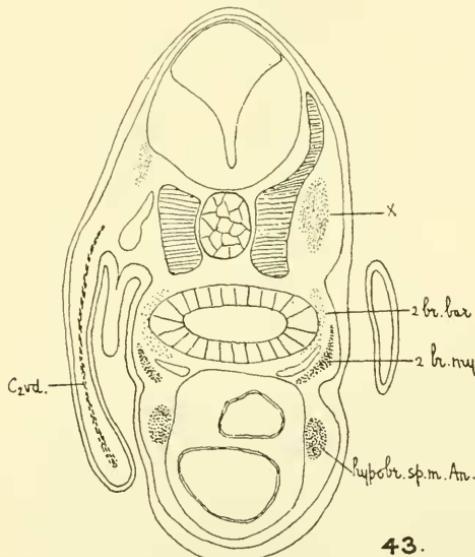
It is of interest to note that in Siren (Drüner) there is a levator hyoidei, a slip of the cephalo-dorso-mandibularis, i. e. in that animal the primary insertion of the muscle is not wholly lost.

The interhyoidens[1] of Necturus spreads backward behind the hyoid bar in the opercular fold, and this posterior part, at first entirely ventral, spreads upwards laterally external to the cerato-hyoideus externus and depressor mandibulæ. There is a similar development of the interhyoidens in Triton, and

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[1] Posterior mylohyoid of Mivart and Miss Platt.

the hinder part gains an attachment to the first branchial bar.[1]

Schultze described the hyoid muscles of the larvæ of Pelobates fuscus as consisting of an orbito-hyoideus, suspensorio-hyoideus, cerato-hyo-angularis, quadrato-angularis,

TEXT-FIG. 44.
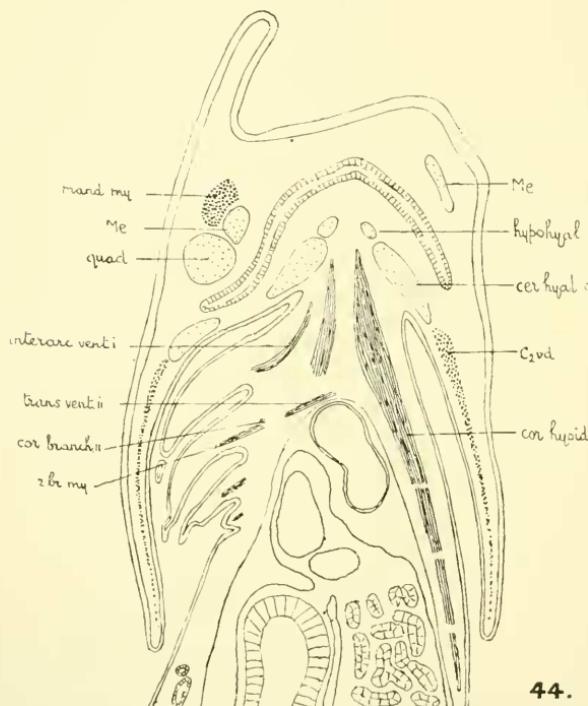
Text-figs. 44 and 45.—Ceratodus, embryo stage 46 ; longitudinal horizontal sections. Text-fig. 44 is the more dorsal ; the left side of the sections is slightly dorsal to the right side.

and suspensorio-angularis. In Rana the myotome of the hyoid segment separates from the interhyoideus in 6 mm. embryos. It divides in 7 mm. embryos into an upper and lower portion (Text-fig. 58) ; the former develops into the orbito-hyoideus, which passes from the processus muscularis of the

[1] First interbranchial of Drüner.

palato-quadrate to the ceratohyal; the latter, which is the
hyomaxillaris, grows forwards to the outer end of Meckel's
cartilage and divides into the cerato-hyo-angularis, suspen-
sorio-angularis, and the quadrato-angularis (Text-fig. 59). In
Bufo lentiginosus the upper portion of the myotome forms
only an orbito-hyoideus, as in Rana; in Pelobates and Alytes it
forms an orbito-hyoideus and suspensorio-hyoideus. In Pelo-

TEXT-FIG. 45.
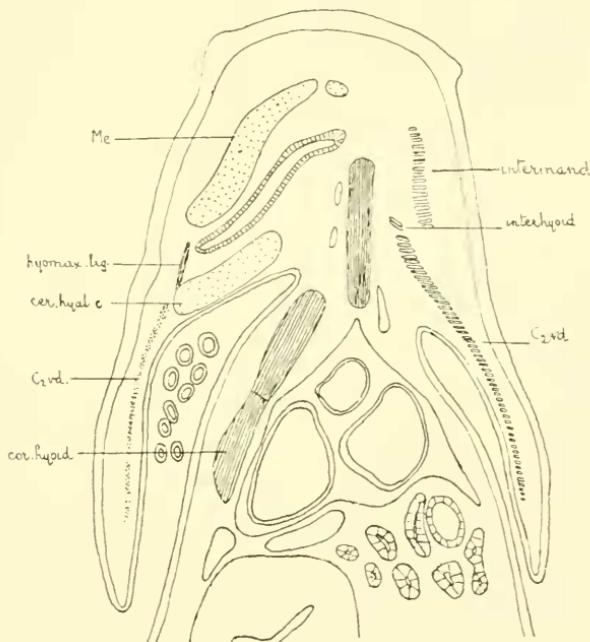
45. [1]

bates and Bufo lentiginosus the hyo-maxillaris divides
into three muscles as in Rana, in Alytes into two only, the
cerato-hyo-angularis and quadrato-angularis (Text-fig. 63).

In Rana, at metamorphosis, the upper end of the orbito-
hyoideus extends upwards on the atrophy of the processus
muscularis of the palato-quadrate; subsequently, on rotation
backward of the palato-quadrate, the lower end of the orbito-

[1] The coraco-mandibularis in this drawing is unfortunately not named.

TEXT-FIG. 46.

46.
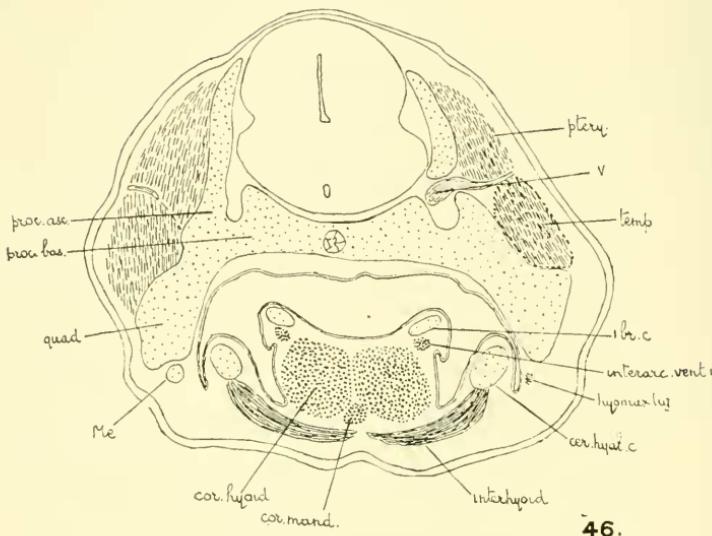
TEXT-FIG. 47.

47.
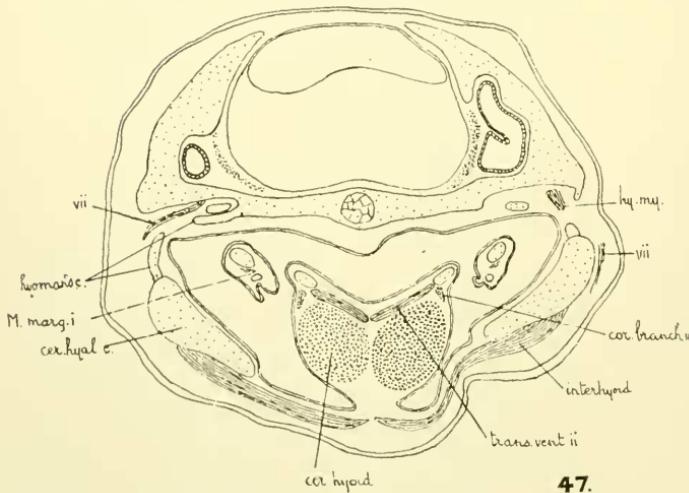
Text-figs. 46–48.—Ceratodus, embryo stage 48.   Text-fig. 46 is
the most anterior.

hyoideus gains a new insertion to the hind end of the lower jaw. The cerato-hyo-angularis, suspensorio-angularis, and quadrato-angularis assume a more vertical position on the rotation of the palato-quadrate, and form the inner portion, whilst the original orbito-hyoidens forms the outer portion, of the depressor mandibulæ.

The interhyoideus of the larvæ of Rana[1] forms a transverse band connecting together the two ceratohyals (Text-fig. 57), and this is also the case in Alytes. In Pelobates and Bufo

TEXT-FIG. 48.
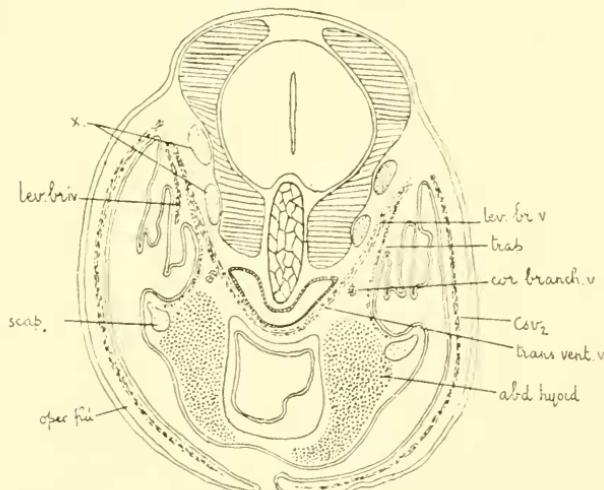
48.

lentiginosus it extends backwards below the branchial cavity, and this hinder part forms the sub-branchialis (of Schultze), and the diaphragmato-branchialis (of Schultze) is separated from the median edge of this muscle.

The digastric muscle[2] of Mammals is either monogastric (digastricus spurius), inserted into the jaw, or digastric (digastricus verus), with a tendon between the two bellies which may or may not be connected with the hyoid bone.

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[1] Subhyoideus of Ecker and Gaup, and of Schultze.

[2] This bare outline only is given, as the matter has been so thoroughly discussed by Bijvoet.

The anterior belly of a digastricus verus is innervated by the Vth, the posterior belly by the VIIth. A digastricus spurius has a deeper or superficial tendinous inscription, and is also innervated by both Vth and VIIth.

Anatomists who have investigated the adult conditions of the muscle have expressed various views as to its origin; some, e. g. His and Chaine, thought that the muscle was developed from one mass; others, e. g. Humphrey, Gegenbauer, Rüge, Fürbringer, Bijvoet, have held that it was developed from two masses.

Bijvoet, the latest investigator of the subject, was of opinion that the condition present in Monotremes—a M. depressor mandibulæ anterior, and a M. stylohyoideus—is the "Ausgangsform," that from this was developed a digastricus verus, and that a digastricus spurius was a secondary condition. He was also of opinion that a M. intermandibularis separated into a M. mylohyoideus and a M. depressor mandibulæ anterior. The only descriptions of the development of the digastric muscle which have hitherto been given are those by Futamura of human and pig embryos. He says that the common Anlage of the digastricus, stylohyoideus, and stapedius is visible in twenty-seven to thirty day human embryos as a "medialwärts sich anhäufende dicht gedrängte Muskelblastemgewebe," which is continuous laterally with the platysma Anlage, the whole forming a single mass. In embryos a little older the platysma and digastric Anlagen separate. In six weeks' embryos the digastric Anlage passes forward to the anterior border of the lower jaw. The mylohyoid nerve at this date passes to the mylohyoid muscle only; it does not innervate the anterior belly of the digastric until the age of seven weeks. The stylohyoid and stapedius begin to separate from the posterior belly of the digastric at the age of six weeks. The digastric is thus solely a facial muscle, the anterior part of which receives a secondary innervation from the trigeminal nerve.

Bijvoet doubted this account given by Futamura, as it appeared to him to disagree with the results of comparative anatomy.

Futamura's account of the development of the facial and platysma muscles is that their Anlage separates, as stated above, from the outer aspect of the common facial Anlage; in thirty-one to thirty-four day embryos it spreads aborally almost to the shoulder region, forming the platysma colli, and in six-week embryos also forwards, in two directions separated by the outer ear, forming a platysma occipitalis and a facial portion. The latter passes forwards over the edge of the lower jaw to the forehead, eyelid, upper lip, and temporal region, separating into a deep and a superficial layer.

In 3 mm. embryos of the rabbit the hyoid myotome is continuous below with the epithelium lining the hyoid section of the cephalic cœlom (Text-fig. 77). In 4 mm. embryos the walls of the cephalic cœlom have come together, and the Anlage of the interhyoideus is formed from its epithelial wall; each half is continuous laterally with the lower end of the myotome (Text-fig. 81). In $7\frac{1}{2}$ mm. embryos the myotome is partially separated into an upper and a lower part; the former is the Anlage of the posterior digastric, stylohyoid, and stapedius, the latter that of the anterior digastric (Text-fig. 89). In embryos between 8 and 9 mm. the hyoid bar is formed,[1] and in its whole extent simultaneously, so that there is no stage in which the Anlage of the posterior digastric, stylohyoid, and stapedius is inserted into the upper end of a hyoid bar which has not yet extended up to the auditory capsule. In 9 mm. embryos (Text-figs. 92 and 93) the lateral edge of the inter-

[1] The " body of the hyoid " in the rabbit is formed from the ventral ends of the hyoid and first branchial bars. No basihyal nor basibranchial is developed. In 9 and 13 mm. embryos a column of cells— the remains of the glosso-thyroid duct—extends downwards from the foramen cæcum in the middle line between the hyoid and first branchial bars. Antero-posterior fusion of the ventral ends of these bars to form the body of the hyoid, and the commencement of formation of a joint between the body and the first branchial cornua, take place in embryos between the stages of 13 and 17 mm. Chondrification takes place later in the " body " than in the hyoid and first branchial cornua. These findings confirm the suggestions of Parsons; in the rabbit, however, there is no basihyal.

hyoideus has separated from and extended upwards outside the
anterior digastric, which has grown a little forwards. In 10
mm. embryos the anterior end of the anterior digastric has
reached Meckel's cartilage, the interhyoidens has extended
forwards, and also backwards in the neck forming the platysma
colli, and the stapedius has separated from the Anlage of the
posterior digastric and stylohyoid. In 13 mm. embryos the
Anlage of the posterior digastric and stylohyoid has separated
into those muscles, and the lateral edge of the fore part of the
interhyoideus (Text-fig. 96) has extended upwards and for-

TEXT-FIG. 49.
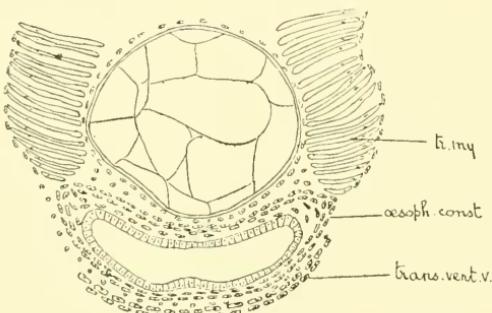
49.

Text-fig. 49.—Ceratodus, embryo 15 mm.; portion of transverse
section taken between the fifth branchial segment and the lung.

wards forming the platysma occipitalis and platysma faciei.
The posterior digastric forms a tendon (vide Krause).

There is thus in the rabbit a stage of development prior to
the first described in man by Futamura, in which the Anlage
of the platysma faciei, platysma occipitalis, and platysma
colli is a structure homologous with the interhyoidens of lower
forms. The anterior digastric is homologous with the hyo-
maxillaris of some Amphibia and Teleostomi.

The Homologies of the Hyoid Muscles.—In Alytes,
Bufo, Rana, Pelobates, and Lepus, the lower end of the hyoid
myotome becomes separated from the part above and forms
a longitudinal muscle—the hyo-maxillaris—connecting the
hyoid bar with the lower jaw. An homologous muscle is

formed in Amia and Salmo, but differs in that it is separated from the upper end of the hyoideus inferior. The first mentioned method of formation is probably the primitive one, for serially homologous muscles, interarcuales ventrales, are formed from the lower ends of branchial myotomes where there are no muscles homologous with the interhyoideus; the method of formation in these Teleostomi is probably related to the secondary position of the adductor hyomandibularis internal to the upper part of the hyoid bar. In Urodela (Necturus, Triton), Ceratodus, Lepidosteus, and

TEXT-FIG. 50.
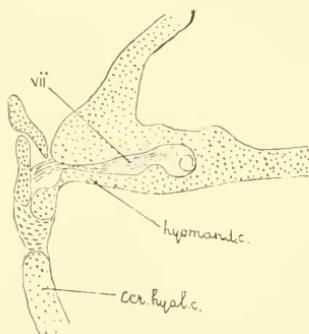
50.

Text-fig. 50.—Ceratodus, advanced embryo. length ?: portion of transverse section, to show relations of the hyomandibular cartilage.

Acipenser a corresponding Anlage develops into a hyomaxillaris ligament. In Selachii (Scyllium, Acanthias) and in Sauropsida no hyo-maxillaris Anlage is formed.

The developmental history of the hyo-maxillaris suggests that its primitive condition was that of a longitudinal muscle passing from the hyoid bar to the hind end of Meckel's cartilage, but this is not preserved in any of the animals investigated. In Teleostomi (Amia and Salmo) the front end of the muscle extends forwards along Meckel's cartilage.

In Chimæra there is a similar muscle (hyoideus inferior of Vetter) extending from the hyoid bar along the lower jaw.

In Rana, at metamorphosis, the muscle becomes more vertical in position, and forms, with the orbito-hyoideus, the depressor mandibulæ ; this stage is preceded by a larval one, in which the muscle, having a longitudinal direction, is in part attached to the palato-quadrate bar. In Mammals the hyo-maxillaris (anterior digastric) may lose its attachment to the hyoid bar and form part of a digastricus verus with a tendon not attached to the hyoid bar, or part of a digastricus spurius.

The part of the hyoid myotome above the hyo-maxillaris in cases where this is formed, or above this and the cerato-hyoideus externus (in the Urodela), or the whole myotome, where either or both of these muscles is not formed, is at first wholly or partially (Scyllium) inserted into the upper end of a hyoid bar, which has, or has not yet, extended up to the auditory capsule, forming a levator hyoidei. This holds for Scyllium, Acipenser, Lepidosteus, Amia, Salmo, Ceratodus, Necturus, Triton, Rana, and other Anuran larvæ, Chrysemys, and Gallus. In the Amphibia the hyoid bar remains in this primitive condition, in the other groups it extends upwards to the auditory capsule.

According to Kingsbury and Reed, the columella auris of Urodela is the homologue of the hyomandibula of other forms. If this be so, its dorsal relation to the seventh nerve would suggest that it is homologous with the hyomandibula of Teleostei, where a similar relation holds, rather than with that of Selachii, Ceratodus, and Sauropsida, which lies ventral to the VIIth.

Against such homology, however, it might be urged that in Scyllium, Acipenser, Lepidosteus, Amia, Salmo, Ceratodus, Chrysemys, and Gallus (Geoffry Smith), the hyomandibula is formed by a secondary segmentation occurring in a hyoid bar, which extends continuously up to the auditory capsule, whereas this is not stated by Kingsbury and Reed to occur in Urodela.

A levator hyoidei—attached to the upper end of a hyoid bar—is not preserved to adult life in any of the animals examined. In Urodela and Sauropsida it extends downwards

TEXT-FIG. 51.
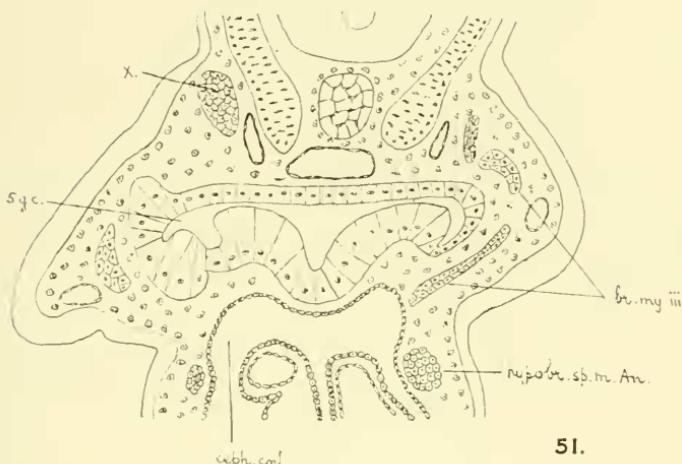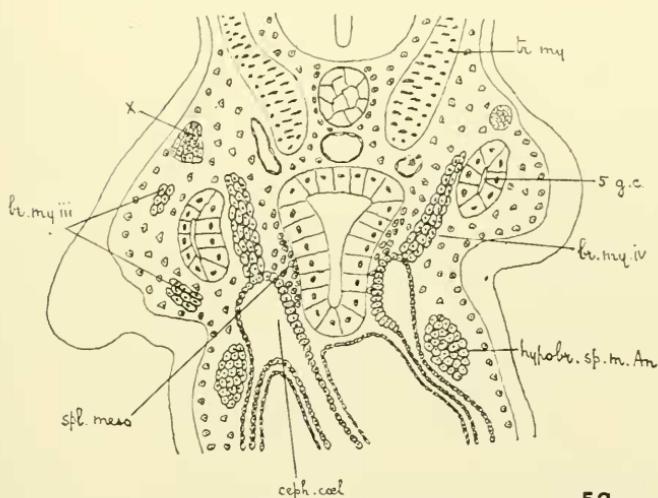
TEXT-FIG. 52.

Text-figs. 51 and 52.—Necturus. embryo 12 mm. Text-fig. 51
is the more anterior.

to Meckel's cartilage, forming the depressor mandibulæ. In Rana this also occurs at metamorphosis, the muscle forming the outer part of the depressor mandibulæ. In Scyllium the levator hyoidei, on the upgrowth of the hyoid bar, is inserted into its outer surface, and in very late stages of development extends forwards to the quadrate. In Teleostomi, on the upgrowth of the hyoid bar, the levator hyoidei becomes inserted into its posterior edge or inner surface, and in Salmo additionally spreads forward to the palato-quadrate. In Ceratodus the insertion of the levator hyoidei to the upper end of the ceratohyal is lost, but it is preserved in Protopterus (vide description by Ruge). In Lepus there is no stage in development in which there is a levator hyoidei inserted into the upper end of a hyoid bar, for this is formed simultaneously in its whole length, but the portion of the myotome above the Anlage of the hyo-maxillaris (anterior digastric) is a mass, which is homologous with the levator hyoidei of other forms, and lies outside the hyoid bar ; it subsequently divides into stapedius, stylohyoideus and digastricus posterior. It is homologous with the M. styloideus of Monotremes. The upper end of the levator hyoidei is attached to the auditory capsule ; this attachment, in Anura, is preceded by a larval stage, in which the upper end of the muscle takes origin from the processus muscularis of the palato-quadrate bar.

The primary form of the interhyoideus—formed from the walls of the obliterated hyoid section of the cephalic cœlom, and serially homologous with the intermandibularis—would appear to have been a transverse band connecting the two hyoid bars, but in all forms examined, other than Rana and Alytes, it extends backwards. In Urodela, Anura, and rabbit there is a backward extension of the interhyoideus only, but in Selachii, Teleostomi, Ceratodus, and Sauropsida, of both myotome and interhyoideus, forming a continuous ventro-dorsal sheet (C_2vd of Ruge) behind the hyoid bar. The backward extension of the interhyoideus, or of this and of the myotome, takes place in the opercular fold in Urodela, Anura, Ceratodus, and Teleostomi ; in part in the opercular

Text-fig. 53.
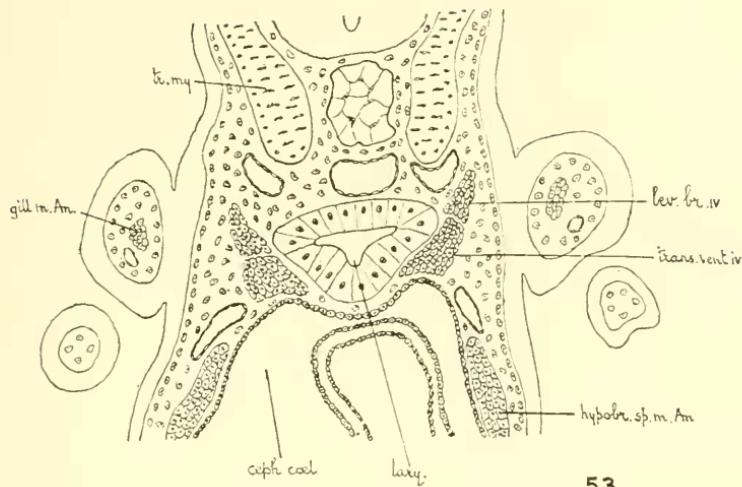
53.

Text-fig. 54.
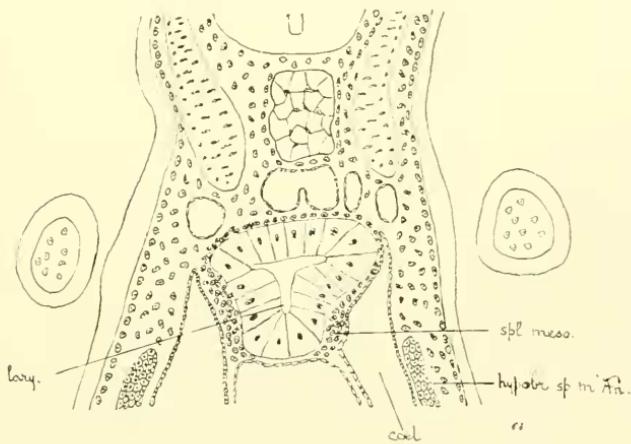
54.

Text-figs. 53 and 54.—Necturus, embryo 13 mm., transverse
section. Text-fig. 53 through the fourth branchial segment,
Text-fig. 54 a little more posterior.

fold (only existing ventrally) in Sauropsida and rabbit; and in Scyllium entirely in the wall of the head, no opercular fold, even as an atrophying Anlage, being developed.

The backward extension of the interhyoideus forms the hinder part of the interhyoideus of Urodela, and the sub-branchialis of Anura. In the rabbit the attachment of the interhyoideus to the hyoid bar is lost, and it spreads down the neck, forming the platysma, and also upwards and forwards, forming the superficial occipital and facial muscles.

C_2vd persists as a continuous ventro-dorsal sheet in Scyllium, Ceratodus, and Sauropsida; in the latter group, in correlation with the atrophy of the gill-clefts, it spreads backwards in the neck, forming the constrictor colli; in Teleostomi it separates into dorsal and ventral portions, the former developing into the opercular muscle or muscles, the latter into a constrictor operculi (Acipenser and Polypterus), or hyohyoideus superior (Lepidosteus, Amia, Salmo).

The hinder part of the interhyoideus of Urodela and the platysma of the rabbit imitate, to some extent, the constrictor colli of Sauropsida, but this is due to a dorsal extension of their lateral edges over the hyoid myotome after their formation from the interhyoideus only.

It will be shown, later, that the probable primitive condition of the muscles of each branchial arch was, a M. levator, a M. marginalis, a M. interarcualis, and a M. transversus ventralis. The levator hyoidei is serially homologous with the first, and the hyo-maxillaris with the third of these. The cerato-hyoideus externus is serially homologous with the Mm. marginales and their homologues the Anlagen of the gill-muscles, and may possibly be derived from a hyoidean M. marginalis, but there is no trace of such a muscle in other groups. There are no homologues of the transversi ventrales in the mandibular and hyoid segments.

The primitive condition of the mandibular and hyoid muscles was probably one in which the former lay wholly in front of the latter. This condition exists in the embryo but does not persist; during development, in correlation with the

TEXT-FIG. 55.
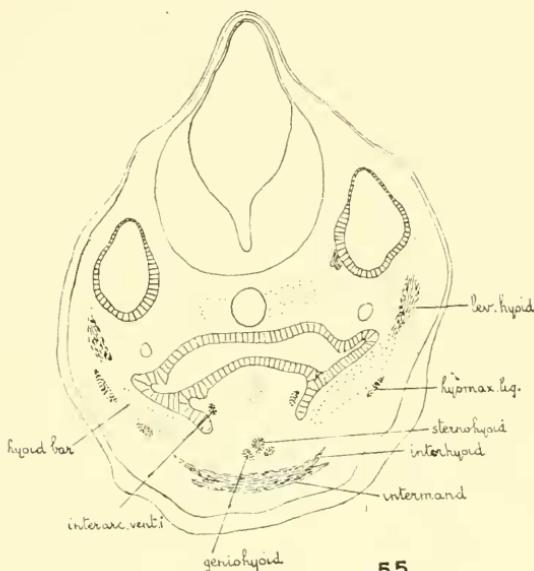
55.

TEXT-FIG. 56.
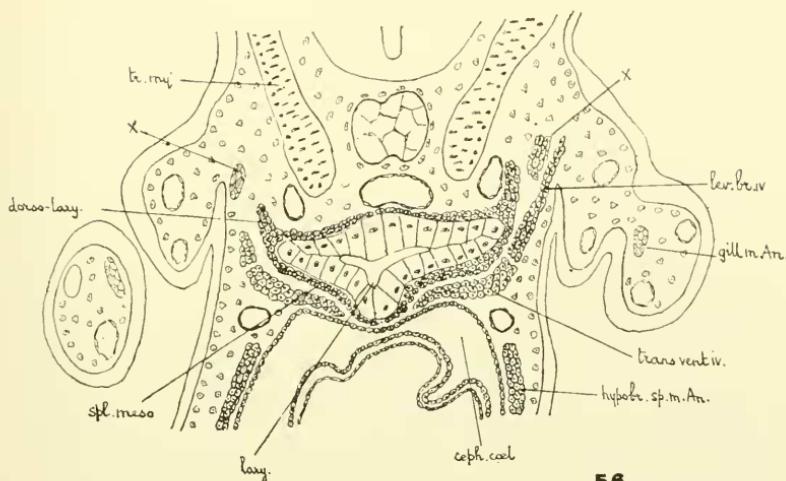
56.

Text-figs. 55 and 56.—Necturus, embryo 14½ mm., transverse
sections. Text-fig. 55 through the hyoid segment, Text-fig. 56
through the fourth branchial segment.

increase in size of the jaws, there is a gradual overlapping of the hyoid bar by the mandibular skeletal structures, with associated secondary changes in the muscles. Thus, the levator hyoides shifts its insertion from the hyoid bar to the hind end of Meckel's cartilage in Amphibia and Sauropsida, and the intermandibularis partially underlies the interhyoideus in Selachii, Teleostomi, Ceratodus, and Urodela. It is probably in connection with this overlapping that the hyomaxillaris Anlage becomes a ligament in Urodela, Ceratodus, and some Teleostomi, and is not developed in Selachii and Sauropsida.

Eye Muscles of the Rabbit.

The development of the external ocular muscles in Teleostoman and Amphibian embryos was not followed.

In pig embryos of 10 mm. maximum and 6 mm. Nackenlänge, Reuter found the Anlage of the eye muscles as an "untrennbarer Zellcomplex," which, he held, "als Anhaufung von morphologisch ursprünglich Keimzellen aus dem Mesenchym hervorgeht."

In 3 mm. embryos of the rabbit the premandibular Anlage is developed, on each side, as a hollow outgrowth of the fore end of the alimentary canal (Text-fig. 75). This outgrowth becomes solid by proliferation of its walls as it is constricted off, and in $3\frac{1}{4}$ mm. embryos (Text-fig. 79) it forms a solid mass connected with its fellow by a solid string of cells lying across the fore end of the alimentary canal just below the anterior down-turned end of the notochord. The connecting string of cells has disappeared in $4\frac{1}{4}$ mm. embryos. The premandibular Anlage forms a crescent-shaped mass in 4 mm. embryos (Text-fig. 84); and from this the recti superior, inferior, internus, and obliquus inferior are formed (Text-figs. 96, 97). The obliquus superior is formed from the anterior extremity of the upper end of the mandibular myotome in $3\frac{1}{4}$ mm. embryos (Text-fig. 78). The development of the abducens Anlage is doubtful; in $3\frac{1}{4}$ mm. embryos it is visible lying

behind the premandibular Anlage and internal to the mandibular myotome (Text-fig. 79). In $2\frac{1}{2}$ mm. embryos it apparently is represented by a group of cells lying above the first gill-cleft and continuous behind with cells lying in the hyoid segment—cells which in 3 mm. embryos have differentiated into myotome and surrounding mesoblast. It is probable, therefore, that the abducens Anlage is formed from the mesoblast of the hyoid segment before the myotome is

TEXT-FIG. 57.
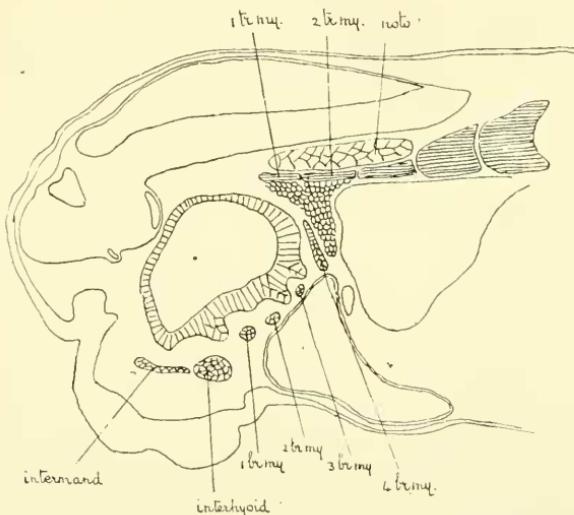
57.

Rana, embryo 6 mm., longitudinal vertical section.

formed. The abducens Anlage begins to separate into rectus externus and retractor oculi in 13 mm. embryos (Text-fig. 96).

These observations suggest that perhaps in pig embryos of a younger age than those investigated by Reuter a similar series of events may occur. In the later stages of development there is also a difference between the pig and the rabbit; in the former, according to Reuter, the retractor oculi is formed from all four recti, in the latter it is formed from the abducens Anlage only, as is usual in Vertebrates.

BRANCHIAL MUSCLES.

The homologies between the branchial muscles of various vertebrates are obscured by the absence of uniformity in nomenclature. The word "interbranchial" has been applied to many quite different muscles. It was used by Vetter to denote the layer of muscle-fibres which lies external to the branchial bars and internal to the superficial constrictor in Selachii. It was subsequently employed by Bronn and by Schultze to denote longitudinal muscles between the ventral ends of branchial bars in Amphibia; by Drüner, to denote transverse muscles in Amphibia; by K. Fürbringer and by Greil to denote slender vertical muscles in Ceratodus.

In this paper the word "interbranchial" is used exclusively in the Selachii in the sense of Vetter; longitudinal muscles between the ventral ends of branchial bars are called "interarcuales ventrales" (vide infra); transverse muscles are called "transversi ventrales," and the vertical muscles of Ceratodus are called Mm. marginales, as they are exactly homologous with the Mm. marginales of Anuran larvæ described by Schultze.

Fürbringer included two sets of muscles under the term "hypobranchial spinal musculature"[1]—(1) Those which are sometimes called ventral longitudinal muscles, e. g. coraco-mandibularis, coraco - hyoideus, genio - hyoideus, sterno-hyoideus; (2) the coraco-branchiales of Elasmobranchs, Teleostomi, and Dipnoi.

Investigation of the development of these muscles, however, shows that whereas the ventral longitudinal muscles are derived from trunk-myotomes, the coraco-branchiales are derived from the ventral end of one or more branchial myotomes, i. e. are of cranial origin. The above-mentioned terminology would therefore appear to be in need of revision,

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[1] The name "hypoglossal musculature" employed by Neal and by Corning has nearly, but not quite, the same meaning as Fürbringer's "hypobranchial spinal musculature," e. g., it would include the cerato-hyoideus (interarcualis ventralis I) of Sphenodon.

and in this paper longitudinal muscles derived from trunk-myotomes are called "hypobranchial spinal muscles," and longitudinal muscles derived from branchial myotomes are called "hypobranchial cranial muscles."

The Anlagen, which in some Vertebrates grow backwards and form coraco-branchiales, are homologous with Anlagen in other Vertebrates, which form muscles passing between the ventral ends of the branchial bars. Many different
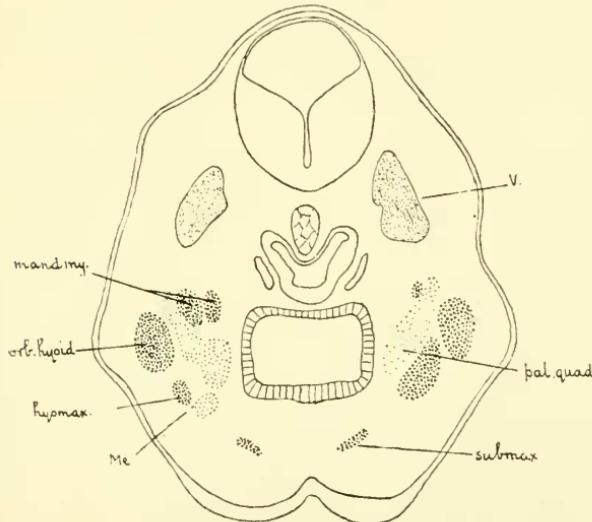
TEXT-FIG. 58.

Rana, embryo 7 mm., transverse section.

names have been given to the latter muscles, e.g. inter-branchiales s. constrictores arcuum branchialium (Bronn), constrictores arcuum (Mivart), interbranchiales (Schultze), subarcuales (Drüner).

Vetter called certain muscles in the branchial arches of Acipenser "interarcuales ventrales," and gave the name of "obliqui ventrales" to exactly homologous muscles in Teleostei. One or other term is superfluous, and following Allis, that of "obliqui ventrales" is used in this paper for the Teleostomi generally. The name "interarcuales ventrales"

is used for the longitudinal muscles passing between the ventral ends of the branchial bars.

The foremost "interarcualis ventralis" passing from the first branchial to the hyoid bar has received many names, e. g. ceratoïdien latéral on petit ceratoïdien (Cuvier), inter-cornalis (Owen), cerato-hyoideus internus (Fürbringer, Miss Platt, Drüner), cerato-hyoideus (Osawa), hyoideus lateralis (Bendz), kerato-hyoideus (Ellenberger and Baum), inter-hyoideus (Dubois), kerato-thyro-hyoideus (Jaquet). The name "branchio-hyoideus" was applied to this muscle in Sphenodon (loc. cit.), and is employed in the case of other animals, when it occurs, in this paper.

In Scyllium, van Wijhe described the coraco-branchialis and coraco-mandibularis as developing from the walls of the obliterated anterior prolongation of the pericardium, and from "Nebenzweige," given off from the "Unterenden der Wände der Visceralbogenhöhlen."

It will be shown later (p. 268) that the coraco-mandibularis and coraco-hyoideus are developed from the fourth to eighth trunk-myotomes. The five branchial myotomes form at first epithelium-lined cavities continuous below with the cephalic cœlom (Text-fig. 2). They separate from the cephalic cœlom in 14 mm. embryos, and their cavities become obliterated (Text-fig. 4). In 17 mm. embryos the lower ends of the branchial myotomes grow backwards, and become cut off from the remainder of the myotomes, forming coraco-branchiales (Text-figs. 8, 10). The (now) ventral ends of the myotomes grow downwards outside the Anlagen of the coraco-branchiales forming the ventral ends of the constrictor (Text-fig. 13). The upper ends of the myotomes, in embryos between the lengths of 17 and 20 mm., increase in antero-posterior extent (Text-fig. 14), and, fusing together, extend backward as the trapezius[1] to the shoulder-girdle. Below

[1] It is stated by van Wijhe that the seventh, eighth and ninth myotomes give rise to "Vom Schädel zum Schultergurtel ziehende Muskeln nebst dem vordersten Theile des sterno-hyoideus," but the trapezius is not specifically mentioned by him.

the Anlagen of the trapezius each branchial myotome forms
a transversely broad plate in the branchial septum (Text-fig.
9). The part internal to the branchial bar forms the adductor
(Text-fig. 15) ; the part external to the bar forms—next the
bar, dorsally the arcualis dorsalis[1] (Text-fig. 14), and below
that the interbranchial, whilst the external edge forms the
constrictor superficialis.

In Acipenser the lower ends of the branchial myotomes

TEXT-FIG. 59.
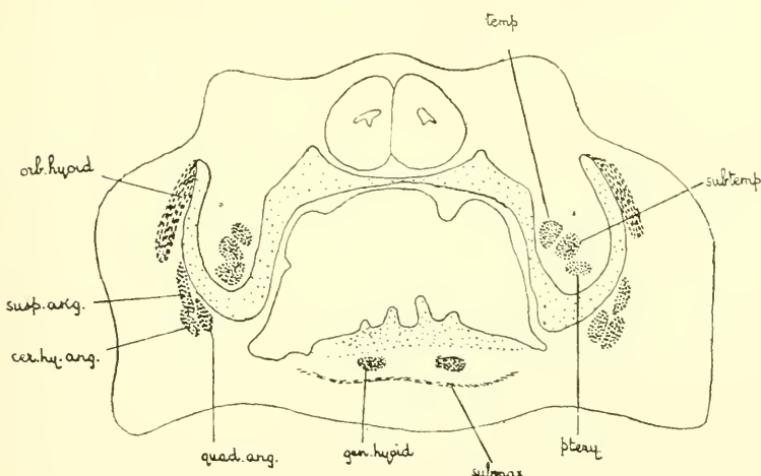
59.

Rana, larva 12 mm., transverse section.

separate from the cephalic cœlom, and in $8\frac{1}{2}$ mm. embryos
(Text-fig. 22) grow downwards, except in the fourth branchial
segment,[2] forming the Anlagen of the coraco-branchiales,
and also downwards and inwards dorsal to the cephalic cœlom,
forming the lower parts of the obliqui ventrales. The ventral
end of the lower part of obliquus ventralis I becomes attached

[1] Employing Fürbringer's terminology (vide p. 266).
[2] In the adult forms examined by Vetter the coraco-branchialis
IV was absent, and it was not developed in the embryos examined.
According to Fürbringer it is present.

to the ceratohyal, and those of the obliqui ventrales II and III to the corresponding hypobranchials, whilst the IVth and Vth meet their fellows in the median line, in the case of the IVth also becoming attached to the basibranchial. The parts of the first three branchial myotomes above the Anlagen of the coraco-branchiales form adductors internal to the branchial bars, and the upper portions of the obliqui ventrales external to the branchial bars; in the case of the fourth myotome only the upper portion of obliquus ventralis

TEXT-FIG. 60.
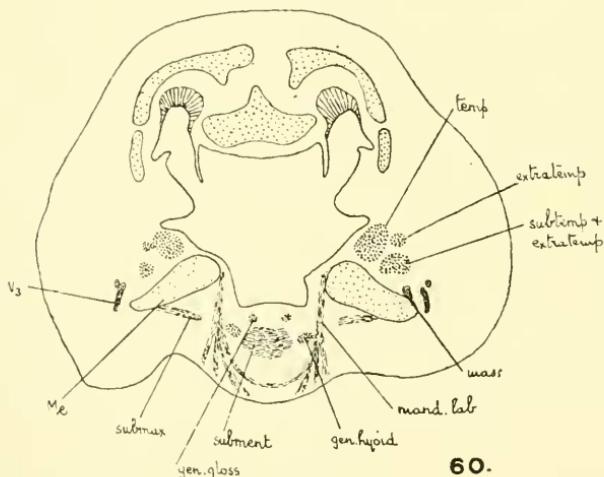
Rana, larva with hind legs moderately developed, transverse section.

IV. The uppermost portions of the first four branchial myotomes form levatores arcuum branchialium; in $8\frac{1}{2}$ mm. embryos the first is attached to the auditory capsule, the second, third, and fourth lie outside the trunk myotomes (Text-fig. 22); in 11 mm. embryos the upper ends of the third and fourth have also shifted to the auditory capsule with additional attachments to the second pharyngo-branchial, and the upper end of the second has become attached to the second pharyngo-branchial; all four are inserted to the corresponding epibranchials. The trapezius is given off from the fourth

levator in $8\frac{1}{2}$ mm. embryos (Text-fig. 22), and grows back to the shoulder-girdle; in 11 mm. embryos its fore part has disappeared, and the anterior end of the part remaining is attached to the skin; in the adult it is absent (Vetter). The portion of the fifth branchial myotome above the coraco-branchialis V forms a muscle attached above the fourth epibranchial and below to the fifth cerato-branchial—the fifth levator of Vetter.

In Amia the lower end of the fifth branchial myotome forms in $8\frac{1}{2}$ mm. embryos (Text-figs. 31, 32) the lateral half of a transversus ventralis V and a coraco-branchialis V, as in Acipenser; the lower end of the fourth branchial myotome forms (Text-fig. 30) the lateral half of a transversus ventralis IV and the Anlage of the interarcualis ventralis IV, which grows forward to the third branchial bar. Neither coraco-branchiales[1] nor interarcuales ventrales are formed in the first three myotomes; the lower ends of the myotomes grow downwards and inwards, forming the ventral portions of the obliqui ventrales I, II, and III. The portion of the fourth myotome, next above the Anlagen of the interarcualis ventralis IV and transversus ventralis IV, forms the obliquus ventralis of that arch, which is serially homologous with the dorsal portions of the obliqui ventrales of the first three arches. In 15 mm. embryos the hind end of the interarcualis ventralis IV grows backward to the fifth bar, and in 19 mm. embryos its front portion divides longitudinally into two (Allis), so that there are formed two longitudinal muscles extending from the third bar to the fourth and fifth respectively; both are innervated by the nerve to the fourth arch (Allis).

Allis homologised these longitudinal muscles with the lower portions of the obliqui ventrales of the first three arches, but their development shows that the latter are homo-

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[1] Fürbringer described a coraco-branchialis II, but it is not described by Allis or McMurrich, and was not present in the embryos examined.

logous with the transversi ventrales of the fourth and fifth arches.

The coraco-branchialis V divides, in 14 mm. embryos, into pharyngo-clavicularis internus and externus.

The upper ends of the first branchial myotomes form levatores arcuum branchialium ; the first two broaden transversely (Text-fig. 29) and divide into external and internal portions. The first and second externi and third and fourth levatores

TEXT-FIG. 61.
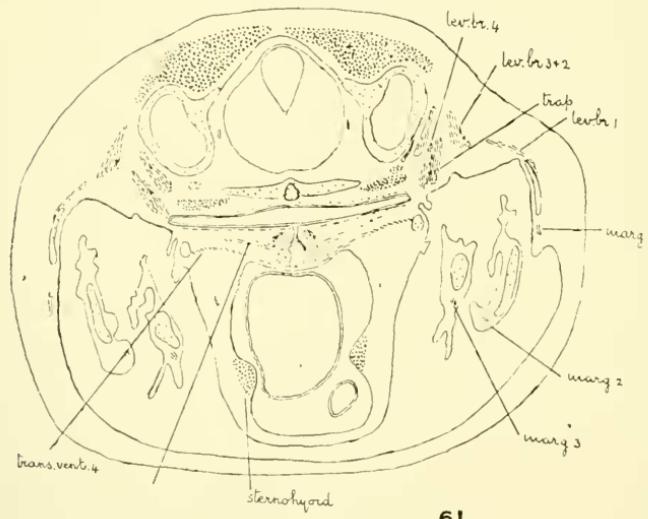
61.

Rana, larva with large hind legs, transverse section.

become attached to the first, second, third, and fourth epibranchials, the first internus to the second pharyngo-branchial, and second internus [1] to the third pharyngo-branchial constituent of the superior pharyngeal bone [2] of Allis (os pharyngeum superior of v. Wijhe, Pharyngealplatte of Wiedersheim). All take their origin from the auditory capsule. The

[1] Protractor laryngis of Wiedersheim.

[2] The os pharyngeum superior of Amia and Lepidosteus (Text-fig. 25) is formed by the union of the pharyngo-branchials of the third and fourth arches—bearing out the theory of v. Wijhe.

trapezius is formed from the fourth levator, and persists; it is the muscle described by Allis as the "fifth externus" levator, "found in 40 mm. fishes as a part of the fourth levator." The portion of the fifth branchial myotome above the coraco-branchialis V does not divide into levator and (dorsal portion of) obliquus ventralis; it forms two muscles— the second obliquus dorsalis and second adductor of Allis, passing from the fourth epi- and cerato-branchial to the fifth cerato-branchial.

The development of the branchial muscles of Lepidosteus is similar to that of Amia, the only exceptions being (1) the coraco-branchialis V does not divide into pharyngo-clavicularis externus and internus (Text-fig. 25)[1]; (2) the interarcualis ventralis IV is not developed.

The differences between the branchial muscles of Salmo and Amia are that in the former (1) the interarcualis ventralis IV retains the primitive condition of a longitudinal muscle between the fourth and third bars, and does not, as in Amia, secondarily extend back to the fifth bar. (2) The third levator arcuum branchialium, as well as the first two, divides into external and internal portions, of which the externus is inserted into the third epibranchial, and the internus into the fourth pharyngo-branchial. (3) The portion of the fifth myotome above the coraco-branchialis V forms one muscle only (obliquus dorsalis of Vetter), passing from the fourth epibranchial to the fifth cerato-branchial. (4) No adductor is formed in the fourth arch.

It is noteworthy that the trapezius persists in Salmo, as in Menidia (Herrick); in Esox, Cyprinus, and Perca it is absent in the adult (Vetter). In some Teleostei there are a greater number of interarcuales ventrales present than in Salmo, e. g. in Cyprinus an interarcualis ventralis I, and in Esox an interarcualis ventralis III are additionally present (Vetter).

The muscles attached to the ventral ends of the branchial bars of Polypterus, apparently, are very different in various

[1] According to Fürbringer, " Lepidosteus hat kein coraco-branchialis mehr."

species. Fürbringer stated that in Polypterus, ? species, there
are four coraco-branchiales attached to the four branchial bars.
Pollard did not describe these; he stated that in Polypterus,
? species, the coraco-hyoideus sends additionally a long
tendon to the lower end of the first cerato-branchial, and also
that there is a muscle belonging to the system of the coraco-
arcuales, which, arising from the fourth, i.e. last cerato-
branchial, passes horizontally forwards and affixes itself to
the lower ends of the second and first cerato-branchiales. It
is apparently supplied by the united first and second spinal

TEXT-FIG. 62.
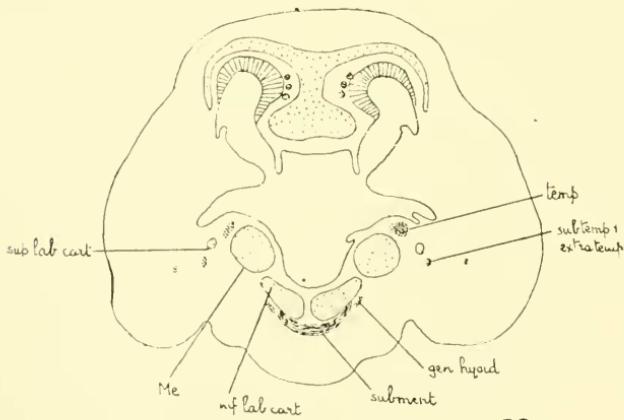
62.

Rana, larva with fully formed hind legs, transverse section.

nerves. There is also "a flat muscle of small size, which
takes its origin from the last cerato-branchial. It loses
itself in the skin near the anterior edge of the dermal clavicle.
Its innervation was not traced."

In Polypterus senegalus (larvæ $7\frac{1}{2}$ to $9\frac{1}{2}$ cm. long)
there is a pharyngo-clavicularis externus and internus (=
coraco-branchialis IV) attached anteriorly to the fourth
cerato-branchial, and passing downwards through the coraco-
hyoideus to the shoulder-girdle (Text-fig. 37). In front of
this is a longitudinal muscle passing from the fourth to the
second cerato-branchial, and innervated by the nerve to the

third arch; this, on comparison with the interarcualis ventralis IV of Amia, is probably an interarcualis ventralis III, which has additionally extended back to the fourth bar. In front of this are the interarcuales ventrales II and I, the former passing from the second to the first cerato-branchial, and the latter from the cerato-branchial to the ceratohyal (Text-figs. 35 and 36).

In Polypterus senegalus there are transversi ventrales III and IV (Text-figs. 36, 37); the median edges of the former are attached to the basibranchial; the latter in its anterior part forms a transverse muscle, and in its posterior part enters into relation with the rima glottidis, forming the dilatator of Wiedersheim. He called the fore part of the muscle M. adductor arc. branch., but adductors, in the sense of Vetter, are not present in Polypterus senegalus, and the whole muscle is a transversus ventralis of the fourth arch.

In Polypterus, ? species, Pollard described four "interarcuales ventrales" (i. e. in the terminology of this paper, "obliqui ventrales"), one to each branchial bar. In Polypterus senegalus these muscles are not present in the first and second branchial segments; in the third and fourth segments their dorsal portions are present in the form of very minute muscles, the lower ends of which are attached to the cerato-branchiales (Text-fig. 37). Pollard described four levatores arcuum branchialium inserted into the upper ends of the cerato-branchials. In Polypterus senegalus the first is inserted into the first pharyngo- and epi-branchial, the second and third into the respective pharyngo-branchials, and the fourth, which has an additional head from the third pharyngo-branchial, into the fourth cerato-branchial. According to Pollard, there is no trapezius corresponding to that of Selachians, but he mentions that a muscular slip—presumably of the fourth levator—continues on beyond the last (fourth) cerato-branchial, and is inserted into the skin-ligaments in front of the shoulder-girdle. In Polypterus senegalus there is a trapezius arising in common with the fourth levator and passing back to the shoulder-girdle (Text-fig. 37).

The development of the branchial muscles of Ceratodus, as given by Greil, is summarised above (pp. 175 and 176). In the specimens examined the lower ends of the branchial myotomes separate from the lateral wall of the cephalic cœlom in stage 42 (Text-figs. 42, 43). In stage 46 the lower end of the first branchial myotome grows forward to the hypohyal (Text-fig. 44), forming the interarcualis ventralis I[1] s. branchio-hyoideus;

TEXT-FIG. 63.
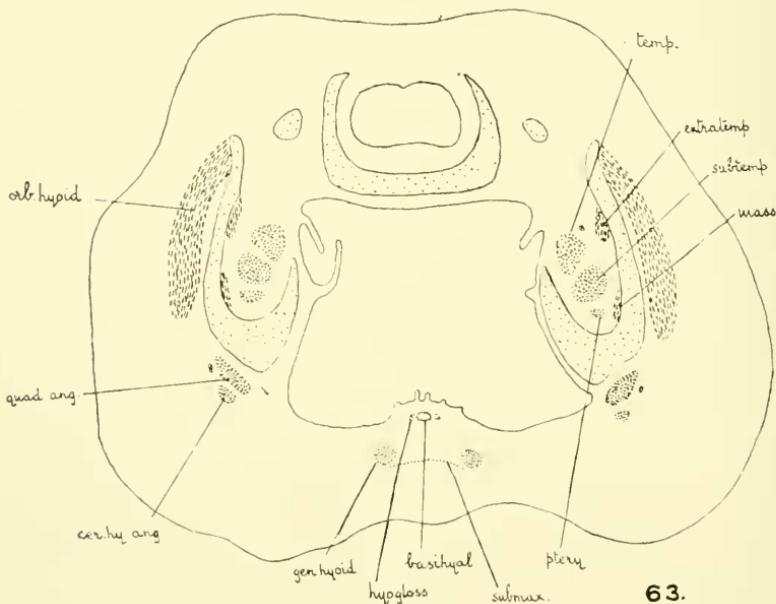
Alytes, larva 12 mm., transverse section.

in the second, third, and fifth branchial segments the lower ends of the myotomes grow downwards, forming coraco-branchiales II (Text-fig. 47), III and V, and also downwards and inwards, forming the (lateral halves of the) transversi ventrales

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[1] Cerato-hyoideus internus of Fürbringer; cerato-hyoideus of Greil; M. grand abducteur du premier arc branchial of Jaquet, who states that the hind end of the muscle is attached to the first and second branchial bars.

II,[1] III,[1] and V [2] ; in the fourth branchial segment only a coraco-branchialis IV is formed. This condition—of an interarcualis ventralis I and coraco-branchiales II, III, IV, and V—persists till stage 63 ; at a later stage the hinder end of the interarcualis ventralis I grows backwards, forming, in the specimen examined, a longitudinal muscle, which is attached posteriorly to the fifth bar, and also a coraco-branchialis I. From this and the descriptions given of the adult by M. Fürbringer and by Jaquet, it may be inferred that the hind end of the interarcualis ventralis I always grows back, forming a coraco-branchialis I, and may or may not also grow back to a more posterior branchial bar.

The portions of the branchial myotomes immediately above the interarcualis ventralis I and coraco-branchiales II, III, and IV form Mm. marginales.[3] No adductors are developed. The upper ends of the first four branchial myotomes and the whole of the fifth branchial myotome above the coraco-branchialis V (no fifth M. marginalis being developed) form levatores arcuum branchialium[4] (Text-fig. 48).

The trapezius[5] is proliferated from the outer side of the fifth levator in stage 48 (Text-fig. 48).

In Necturus (Miss Platt), in embryos of $12\frac{1}{2}$ mm. there is an outgrowth from the ventral part of the glosso-pharyngeal muscle—the beginning of the cerato-hyoideus internus ; and there are three constrictors arcuum, the first growing forwards from the mesothelium of the first vagus arch where this joins

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[1] M. chiasmique of Jaquet ; second and third Mm. interbranchiales of Greil.

[2] The posterior margin of the transversus ventralis V in stage 63 underlies the lung.

[3] M. branchialis of Jaquet ; first, second, third, and fourth Mm. interbranchiales of K. Fürbringer ; fourth and fifth Mm. interbranchiales of Greil. In the adult, according to Jaquet, these muscles are attached dorsally to the upper ends of the branchial bars, according to K. Fürbringer to the skull.

[4] Cranio-branchiales of Jaquet ; levatores arcuum branchialium of Greil.

[5] M. scapulo-branchialis of Jaquet ; levator scapulæ of Greil.

the wall of the pericardium, the second and third arising as a single muscle from the wall of the pericardium in the region where the mesothelium of the second vagus arch unites with the pericardial wall. Above these muscles are found the gill-muscles, and dorsally the three levatores arcuum.

This would mean, according to the theory which was suggested above, that the interarcuales ventrales I, II, and III are formed from the ventral ends of the first, second, and third branchial myotomes, the Anlagen of the gill-muscles above these, and the three levatores from the upper-most portions.

There are three other branchial muscles in Necturus which were not mentioned by Miss Platt—the transversus ven-tralis IV,[1] fourth[2] levator arcuum, and the trapezius.[2] In 12 mm. embryos there is present a fourth branchial myotome serially homologous with the first, second, and third (Text-figs. 51, 52). In 13 mm. embryos this has separated from the cephalic cœlom and divided into a fourth levator and lateral half of a transversus ventralis IV (Text-fig. 53) ; in 14½ mm. embryos the lower half of the transversus ventralis IV has spread inwards dorsal to the cephalic cœlom and below the developing larynx to meet its fellow in the middle line (Text-fig. 56).[3] No interarcualis ventralis IV is developed. Trans-versi ventrales are not developed in the first three arches.[3] The trapezius is proliferated from the outer surface of the fourth levator in 16 mm. embryos.

In Triton cristatus the events are similar; an interarcu-alis ventralis IV is developed, in correlation with the formation of the fourth branchial bar. The interarcuales ventrales II, III, and IV become divided into the muscles called sub-

[1] The fourth pharyngo-branchialis of Wilder ; the hyo-pharyngeus of Göppert.

[2] The fourth levator and trapezius were described by Mivart ; the latter, in the terminology of Fürbringer, is a dorso-scapularis.

[3] This confirms the opinion of Göppert that his hyopharyngeus is not formed by fusion of transversi ventrales III and IV, but is only a transversus ventralis IV.

arcuales recti and obliqui by Drüner. The trapezius is a capiti-dorso-scapularis; it is formed by proliferation from the outer surface of the fourth levator in $8\frac{1}{2}$ mm. (just hatched) larvæ.

Drüner described in Urodela a first, third, fourth, and fifth transversus ventralis (called by him "interbranchial") in the territory of the first, third, fourth, and (an atrophied) fifth branchial arches. He also stated that the first is formed by a secondary attachment of the ventral facial muscles to the first branchial arch—this, which is not a true transversus, is described above (p. 215). In Necturus and Triton cristatus a transversus ventralis III is not formed; there is only a IVth. The question whether the laryngei represent a Vth is discussed below. The transversi ventrales were included by Drüner in the ventral head muscles, but they are not serially homologous with the intermandibularis and inter-hyoideus, which are developed from the walls of the cephalic cœlom in the mandibular and hyoid segments, whereas the transversi ventrales are formed by downgrowths of the branchial myotomes dorsal to the cephalic cœlom.

In Rana temporaria the ventral ends of the four branchial myotomes separate from the parts above in $6\frac{1}{2}$ mm. embryos, and form the Anlagen of the four interarcuales ventrales, and in the second, third, and fourth segments the Anlagen of the transversi ventrales. In the first three segments the middle portions of the myotomes form the Mm. marginales and the upper parts the levators. The portion of the fourth myotome above the interarcualis ventralis forms the fourth levator, no M. marginalis being developed.

The median ends of transversi ventrales II and III become attached to the posterior surface of a ventral projection of the first basibranchial (second copula), and their lateral edges to the processus branchialis. The lateral edges of transversus ventralis IV become attached to the fourth cerato-branchial (Text-fig. 61), and their median edges meet in a central raphé, which underlies the fore part of the larynx. There are similar muscles in larvæ of Alytes, Bufo lenti-

ginosus, and Pelobates.[1]   In Rana, at the end of the meta-
morphosis, the transversi ventrales II and III disappear,
whilst transversus ventralis IV persists.

Wilder was of opinion that transversus ventralis IV
(constrictor laryngis, hyopharyngeus of Göppert, Veren-
gerer des Aditus laryngis of Henle) was a derivative of the
intrinsic ring, i.e. of the sphincter laryngis.   Göppert, on
the other hand, thought that it was homologous with the
hyopharyngeus of Urodela, only differing in that it fails
in the larva to be attached to the fourth bar.   This homology
of Göppert is confirmed by the development of the muscles.
In the Anuran larvæ examined the muscle was attached to
the fourth bar.

The Anlagen of the interarcuales ventrales develop into
longitudinal muscles, each extending from the bar of its
segment of origin to the next anterior one.   In 9 mm. larvæ
the interarcualis ventralis I s. branchio-hyoideus divides
longitudinally into two parts, one of which connects the first
branchial bar to the ceratohyal, the other forms with the
interarcualis ventralis II a muscle extending from the second
branchial bar to the ceratohyal.   A similar development of
the interarcualis ventralis I takes place in Bufo lenti-
ginosus, Alytes, and Pelobates.[2]

The Mm. marginales of Alytes, Bufo, Rana, and Pelobates
(vide Schultze), run along the external edges of the corres-
ponding branchial bars ; their dorsal ends are attached to the
external surfaces of the upper ends (below the insertions of the
levators) of their respective bars.   The ventral end of the first
is attached to the second bar—to the processus branchialis of
Schultze, which is formed from the second bar, the ventral

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[1] The transversi ventrales II and III are collectively termed " basi-
hyobranchialis " by Schultze, in Pelobates.

[2] Schultze did not describe the muscle passing from the first
branchial bar to the ceratohyal in older larvæ of Pelobates, but it per-
sists up to the stage of 30 mm.   The interarcuales II and III he
collectively terms the " interbranchial " ; and the muscle passing from
the second bar to the ceratohyal the " cerato-hyo-branchialis."

ends of the second and third to the third bar, just behind its junction with the processus branchialis. In Rana, at the end of metamorphosis, the cerato-branchial portions of the branchial bars disappear and the Mm. marginales also. The upper end of the first levator becomes attached in part to the palato-pterygoid bar and in part to the periotic capsule, the second, third, and fourth to the periotic capsule only (Text-fig. 61). This is also the case in Alytes, Bufo lentiginosus, and Pelobates.[1]

According to Wilder, in Rana clamitans the fourth levator is formed during metamorphosis by division of the dorso-laryngis into the fourth levator, and dilatator laryngis; and this is stated to hold generally in Anura. In Rana temporaria, however, the fourth levator is formed in 7 mm. embryos, and the dorso-laryngens not until $7\frac{1}{2}$ mm., and the two muscles have no genetic connection; and both muscles are present in larvæ of Pelobates, Alytes, and Bufo lentiginosus, of 10, $12\frac{1}{2}$, and 10 mm. respectively, i. e. long before metamorphosis.

In Rana, late in metamorphosis, the partial origin of the first levator from the palato-pterygoid bar is given up, and, on the atrophy of the cerato-branchials and Mm. marginales, all four levators extend downwards, and their lower ends become attached to the body and processus posterior medius of the hyoid bar.

In 12 mm. larvæ of Rana a downgrowth of the lower end of the fourth levator takes place, forming the diaphragmato-branchialis lateralis[2] (of Schultze). Its upper end becomes attached to the fourth bar, its lower end to the diaphragm. It is innervated by the Xth. It is also formed in Alytes,

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[1] Schultze, in older larvæ of Pelobates, described all four levatores as arising from the palato-quadrate bar.

[2] Schultze gave the name "diaphragmato-branchialis medialis" to the muscle called "sterno-hyoid" in this paper. He did not describe the innervation or development of the larval muscles of Pelobates; his names are purely descriptive, and do not imply that he thought that the two muscles "diaphragmato-branchialis" and "medialis" have any genetic connection.

Bufo lentiginosus, and Pelobates, in larvæ of about the same length. In Rana it disappears late in metamorphosis. The trapezius (capiti-scapularis, of Fürbringer; cucullaris, of Ecker and Gaupp) is formed early in metamorphosis from cells proliferated from the outer surface of the fourth levator (Text-fig. 61).

In 6 mm. embryos of Chrysemys marginata there are four branchial myotomes; in 8 mm. embryos (Text-figs. 66–69) the middle portion of the first is very slender and that of the second has disappeared, and the middle and lower portions of the third and fourth have disappeared; the upper end of the fourth has extended back a little in the neck, the upper end of the third has extended back to that of the fourth, the upper end of the second is a separate structure, and the upper end of the first is still connected with the rest of the myotome. In 12 mm. embryos the dorsal ends of the first and second have each grown backwards into the next segment, and there is thus formed a long column of cells which has grown still further backwards into the neck, forming a trapezius—the capiti-plastralis of Fürbringer; the middle portion of the first and the lower end of the second myotomes[1] have disappeared, whilst the lower end of the first forms the interarcualis ventralis I, which, extending from the first branchial bar to Meckel's cartilage, is the branchio-mandibularis.

In Lacerta agilis the dorsal edge of the primitive trapezius extends upwards outside the trunk myotomes of the neck (Text-figs. 70, 71), and in 20 mm. embryos it has divided into dorsal and ventral portions, the capiti-dorso-clavicularis and capiti-cleido-episternalis of Fürbringer. The former is innervated solely by spinal nerves, the latter by the accessorius vagi. Fürbringer concluded from this innervation that the capiti-dorso-clavicularis is a new formation, and that

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[1] The curious persistence for a time of the lower end of the second branchial myotome, after disappearance of the middle portion of the myotome, is in favour of the idea (loc. cit.) that ancestors of the Sauropsida may have possessed an interarcualis ventralis II, passing from the second to the first branchial bar.

the whole muscle is a complex of muscle-metameres,[1] but this inference is not borne out by study of its development.

In Gallus the upper ends of the first and second branchial myotomes separate from the parts beneath on the fourth day (Text-figs. 72, 73). They fuse together and extend backwards in the neck (Text-fig. 74) forming the trapezius
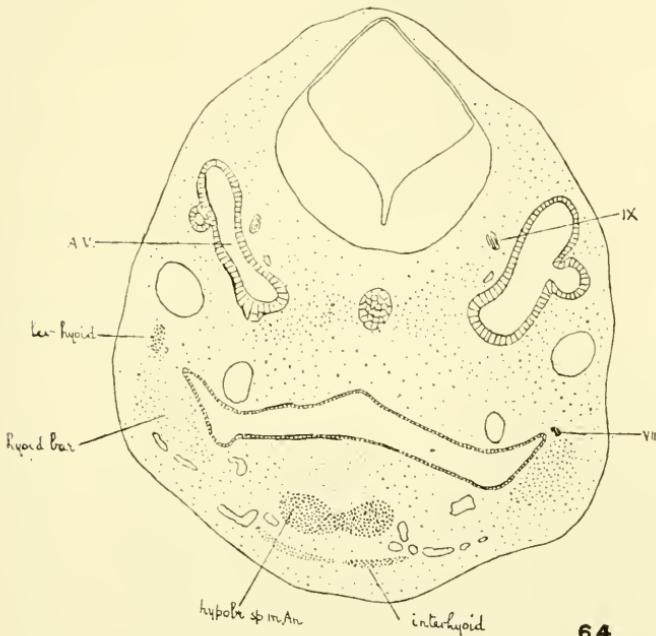
TEXT-FIG. 64.

Text-figs. 64–69.—Chrysemys, embryo 8 mm. Text-fig. 64 is the most anterior; Text-figs. 64 and 65 are through the hyoid segment. Text-fig. 66 through the first branchial, Text-fig. 67 through the second branchial, Text-fig. 68 through the third branchial, and Text-fig. 69 through the fourth branchial segment.

(Cucullaris of Fürbringer). The lower end of the first branchial myotome forms the interarcualis ventralis I s.

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[1] " So entstand ein neugebildeter, dem ursprunglichen M. cucullaris nur in seinen vordersten Theile homologer, in seinen Hauptmasse aber blos imitatorisch-homodynamer oder parhomologer Muskel."

branchio-mandibularis. The middle portion of the first and the whole of the second (below the Anlage of the trapezius) branchial myotomes disappear.

In 5 mm. embryos of the rabbit the upper ends of the first, second, and third branchial myotomes separate from the parts below, the upper end of the third grows backward in the neck, and the upper end of the second backward to join that

TEXT-FIG. 65.
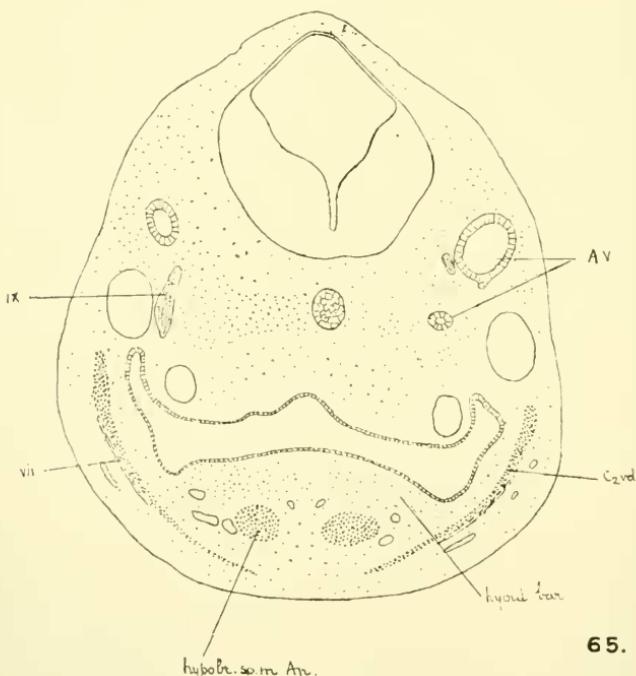
65.

of the third (Text-figs. 85, 86, 87); in 6 mm. embryos the upper end of the first has grown back to that of the second. The hind end of the primitive trapezius, thus formed from the upper ends of all three branchial myotomes, reaches the anterior limb area in 7 mm. embryos (Text-fig. 88); its dorsal edge extends upwards in 7½ mm. embryos (Text-fig. 90), and in 9 mm. embryos it has divided into the trapezius and

TEXT-FIG. 66.
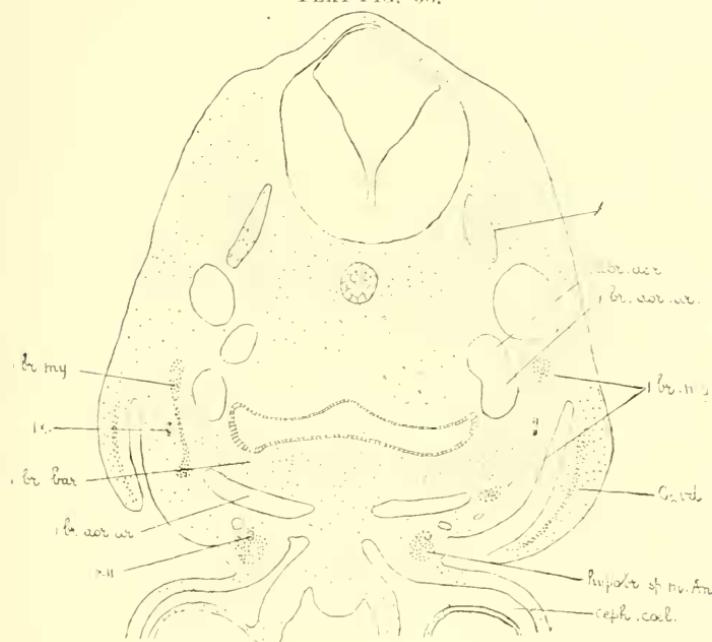
66.

TEXT-FIG. 67.

67.

TEXT-FIG. 68.

68.
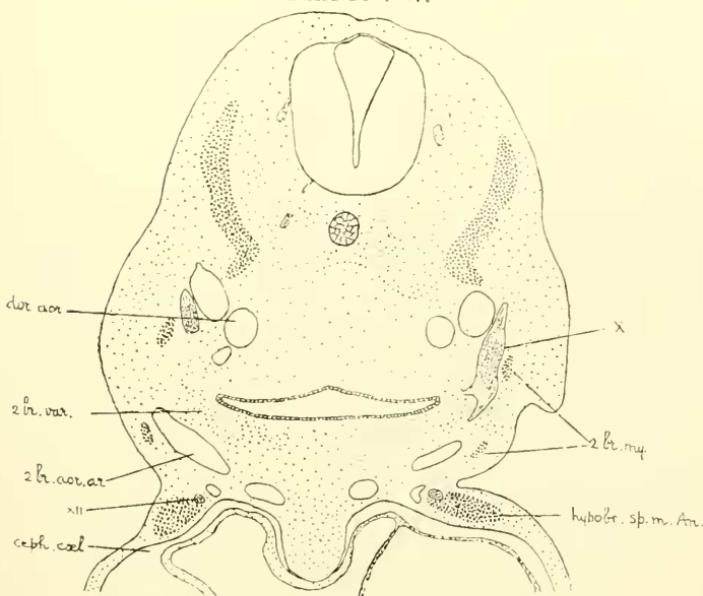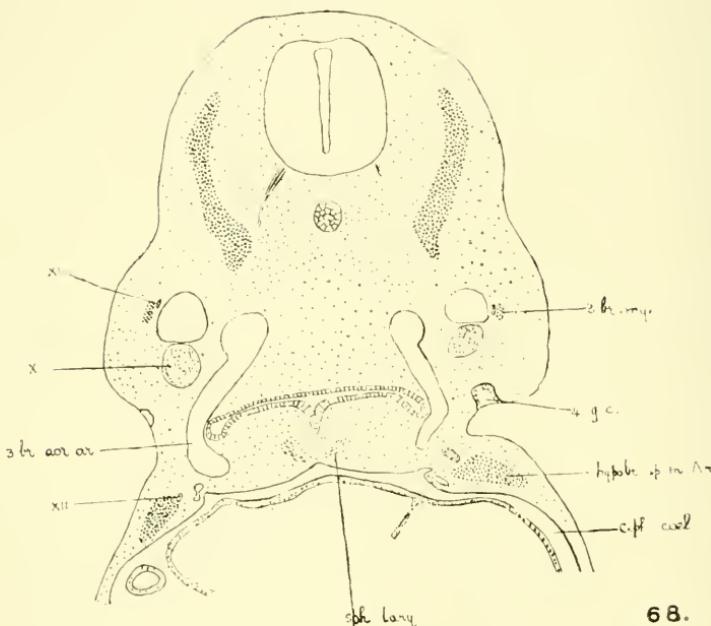
TEXT-FIG. 69.

69.
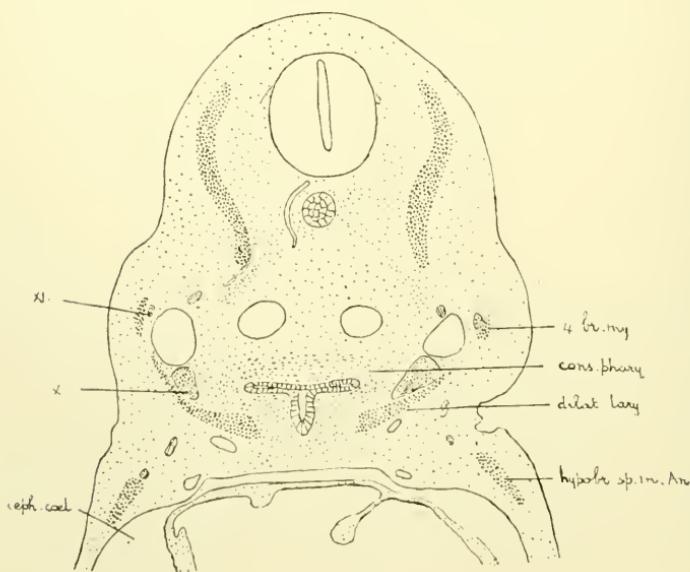
sterno-mastoid of the adult. The portions of the branchial myotomes below the Anlagen of the trapezius have disappeared in 7 mm. embryos.

In the pig the lower end of the first branchial myotome persists (Text-fig. 98), and forms the interarcualis ventralis I s. branchio-hyoideus (Text-fig. 99). This muscle is also constantly present in the dog,[1] and in Monotremes,[2] and is occasionally present in man.[3] In Monotremes there is also an interarcualis ventralis III passing from the third to the second branchial arch.[4]

<center>ON THE HOMOLOGIES BETWEEN THE BRANCHIAL MUSCLES OF VARIOUS VERTEBRATES.</center>

(1) The Hypobranchial Cranial Muscles.—The lower ends of the branchial myotomes develop into longitudinal muscles—interarcuales ventrales, and coraco branchiales—in Selachii, Teleostomi, Dipnoi, Amphibia, and Mammalia. Their innervation varies. Those which remain in their segment of origin, or nearly so, extending forward to the ventral end of the next anterior branchial bar or hyoid bar (or additionally and subsequently to the next posterior bar, in Amia, and probably Polypterus senegalus) are innervated by the corresponding branchial nerve, IXth or branch of Xth, or by this and the next anterior branch. This holds for the interarcuales ventrales of Amia, Polypterus senegalus, Salmo, Ceratodus, Amphibia, and Mammalia. The interarcualis ventralis 1 of Sauropsida (branchio-hyoideus or branchio-mandibularis) is an exception to the rule; it is innervated by the XIIth.

A coraco-branchialis, or pharyngo-clavicularis externus and internus, developed by backward growth from the last branchial myotome, i. e. fourth in Polypterus senegalus, fifth

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[1] Kerato-hyoideus of Ellenberger and Baum.
[2] Interhyoideus of Dubois.
[3] Kerato-thyro-hyoideus of Shattuck.
[4] Interthyroideus of Dubois.

in Amia, Salmo, Esox, Menidia, may either retain its original branchial innervation from the Xth, e. g. Amia (Allis), Esox (Vetter), Menidia (Herrick), Lepidosteus, Polypterus senegalus, or be innervated by spino-occipital nerves, e. g. Amieurus (Wright), Salmo (Harrison). When coraco-branchiales are developed from all the branchial myotomes, they are innervated by the spino-occipital nerves, e. g. Selachii (Vetter, Fürbringer), Acipenser (Vetter), Polypterus ? species (Fürbringer), Ceratodus (Fürbringer).

The coraco-branchiales muscles have been generally classed with the hypobranchial spinal muscles, but investigation of developmental stages shows that the ventral ends of branchial myotomes may form longitudinal muscles, which either grow forwards, forming interarcuales ventrales, or backwards, forming coraco-branchiales, but not in both directions. (There are two, probably three, exceptions to the above rule; in Amia, at a late stage of development, the hind end of the interarcualis ventralis IV grows backward to the fifth bar; the innervation in Polypterus sene-galus suggests that the hind end of the interarcualis ventralis III similarly grows back to the fourth bar; and in Ceratodus the hind end of the interarcualis ventralis I, at a late stage of development, grows back, forming the coraco-branchialis I, and also, at least in some cases, to a more posterior bar.) The first condition, that of interarcuales ventrales, is the primary one, as shown by the correspondence of cranial nerve innervation, with segment of origin. The second condition, that of coraco-branchiales, is a secondary one, in which a change of function to one very similar to that of the coraco-hyoideus is correlated, though in varying degree, with a change of innervation to one by the spino-occipital nerves.

An approximation to what was, probably, the primitive condition, is seen in Amphibia. This was a series of interarcuales ventrales, each extending from the bar of its segment of origin to the next anterior one. The hyo-maxillaris, in the hyoid segment, is serially homologous with

the branchial interarcuales ventrales. There is no homologue in the mandibular segment. These longitudinal muscles possibly date from a period where there were no median cartilages connecting the ventral ends of the hyoid and branchial bars, and formed a rectus system of the head serially homologous with that of the body, though now covered over by the latter, owing to its extension forwards into the head.

TEXT-FIG. 70.
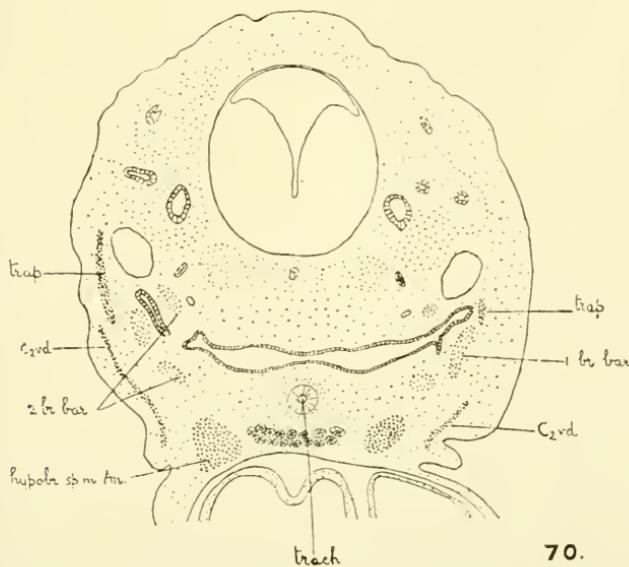
Lacerta, embryo 8 mm., transverse section. The right side of the section is a little anterior to the left.

(1) Transversi Ventrales, Mm. Marginales, and Obliqui Ventrales.—In Scyllium, Acanthias, Sauropsida, rabbit, and pig, the hypobranchial cranial muscles are the most ventral ones formed from the branchial myotomes; no transversi ventrales are formed. This is also the case in the first branchial segment of Anuran tadpoles, the first, second, and third of the Necturus and Triton, the first and fourth of Ceratodus, the first and second of Polypterus senegalus.

But in the second, third, and fourth branchial segments of Anuran tadpoles, the fourth of Necturus and Triton, the second, third, and fifth of Ceratodus, and in those segments of Teleostomi in which hypobranchial cranial muscles are formed, the lower ends of the branchial myotomes also grow downwards and inwards above the cephalic cœlom, towards, or to the middle line forming the (lateral halves of the) transversi ventrales, or their homologues, the lower portions of the obliqui ventrales. In branchial segments of Teleostomi, where hypobranchial cranial muscles are not formed, i. e. first four of Lepidosteus, first three of Amia and Salmo, fourth of Acipenser, there is a similar downward and inward growth of the ventral ends of the branchial myotomes, to form the lower portions of the obliqui ventrales.

The hinder part of the transversus ventralis IV of Polypterus and Amphibia, and of the transversus ventralis V of Ceratodus, comes into intimate relations with the ventral larynx, though in varying ways, underlying it in Amphibia and Ceratodus, forming a dilatator in Polypterus.

The portions of the branchial myotomes next above the Anlagen of the hypobranchial cranial muscles form the Anlagen of the muscles of the external gills in the first three segments of Necturus and Triton, and the Mm. marginales in the first three segments of Anuran larvæ and the first four segments of Ceratodus. Homologous Anlagen form the upper portions of the obliqui ventrales in Teleostoman embryos—of the first four segments of Acipenser, Lepidosteus, Amia, Salmo, Polypterus (Pollard), and of the third and fourth segments of Polypterus senegalus; these may or may not unite with the lower portions. In some segments of Teleostomi, i. e. first three of Acipenser, fourth of Lepidosteus, Amia, and Salmo, adductors are formed from portions of the myotomes lying internal to the branchial bars; they are not developed in Polypterus.

In Scyllium the portions of the branchial myotomes next above the Anlagen of the coraco-branchiales form adductors internal to the branchial bars, and the superficial con-

strictors, interbranchials, and arcuales dorsales external to them. The lower ends of the superficial constrictors extend downwards external to the coraco-branchiales, but such down-growths do not appear to be homologous with the trans-versi ventrales or inferior portions of the obliqui ventrales of Teleostomi, Ceratodus, and Amphibia.

In Sauropsida, rabbit, and pig embryos the portions of the branchial myotomes next above the Anlagen of the hypo-branchial cranial muscles, and also the lower ends where these Anlagen are not formed, atrophy.

Levatores arcuum branchialum are developed from the upper ends of the branchial myotomes in Teleostomi, Cera-todus, and Amphibia, but are not developed in Scyllium, Sauropsida, rabbit, and pig. The method of development of the trapezius—apparently a homologous muscle throughout these vertebrate groups—is intimately related to these differ-ences. It is developed in Teleostomi and Amphibia from the fourth, in Ceratodus from the fifth, levator, i. e. from the penultimate or ultimate levator[1]; whereas in Scyllium, Chrysemys, Gallus, and rabbit, it is formed from the upper ends of the branchial myotomes—five in Scyllium, four in Chrysemys, two in Gallus, and three in the rabbit.

In view of the facts that in Scyllium the subspinalis and interbasales, developed from trunk-myotomes, are attached to the pharyngo-branchials, and that the trapezius is inner-vated only by the XIth—the most posterior of the vagus roots—even though a constituent from the glossopharyngeal (first branchial) segment takes part in its formation, it is probable that the absence of levatores and associated method of development of the trapezius in Scyllium, Sauropsida, and rabbit are secondary phenomena, and that the primary con-dition is a series of levatores formed from the uppermost portions of the branchial myotomes. This theory would also afford an explanation of the curious fact that whereas the

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[1] In Teleostoman embryos the trapezius is developed from the upper edge of the levator, in Ceratodus and Amphibia from its external surface.

general development of the myotomes takes place from before backwards, the separation of the upper ends of the branchial myotomes, their backward growth, and fusion to form a trapezius, in Scyllium, Chrysemys, Gallus, and Lepus, take place from behind forwards—the process beginning in the last branchial myotome.

Adductors of the branchial bars are formed in Scyllium and in certain segments of some Teleostomi, on the inner

Text-fig. 71.
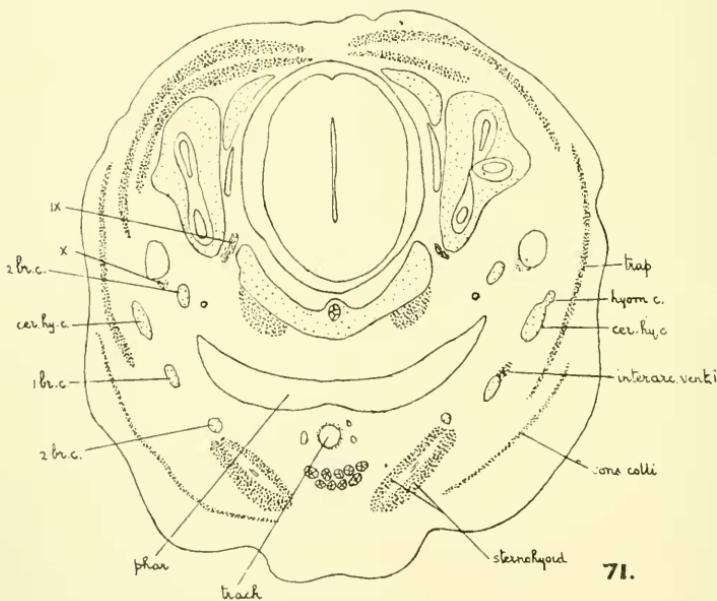
Lacerta, embryo 12 mm., transverse section.

side of the branchial bars. The observations of Balfour[1] showed that the primary situation of the muscles is one external to the bars, so that the non-development of adductors in Amphibia, Ceratodus, and Polypterus would appear to represent a primitive condition.

It may be added that the adductors of the branchial bars are not serially homologous with the adductor mandibulæ, which is formed external to the mandibular arch.

[1] ' Comparative Embryology.' vol. ii. p. 471.

The simplest and probably primary condition of the muscles developed between the levatores above and the hypobranchial cranial muscles below is a series of Mm. marginales, as found in Anuran larvæ and Ceratodus. In Teleostomi these may unite with the (lateral halves of the) transversi ventrales. In Scyllium they undergo a quite special development, which is not found in any other group.

The above comparisons suggest that the probable primitive condition of each of the branchial myotomes was, from above downwards, a levator, a M. marginales, an interarcualis ventrales, and (the lateral half of a) transversus ventralis.

Œsophageal, Pharyngeal, and Laryngeal Muscles. —The term "pharynx" is employed by writers in two senses, either restricted in meaning to the branchial region of the alimentary canal, or including this and the next succeeding portion. In this paper it is used in the first sense.

The œsophagus is surrounded by a circular muscle, the constrictor, which is derived from cells given off from the splanchnic layer of the cœlomic epithelium.

No circular muscles are present in the branchial region of Selachii, Acipenser, and Ceratodus, but are present, in the form of transversi dorsales, in Teleostomi (Vetter), Amia (Allis), and Lepidosteus (Wiedersheim), and are formed by the constrictor of the œsophagus extending forwards, dorsally, into the branchial region. In Polypterus senegalus the fore part of the œsophageal constrictor slightly overlaps the branchial region dorsally, but the transversely directed fibres are not attached to any branchial bar. In Lepidosteus and Amia[1] the conditions are complicated by the presence of a dorsal larynx. The dorsal larynx of Lepidosteus is formed, in 8 mm. embryos, as a solid median upgrowth from the then solid œsophagus just behind the branchial region. The œsophageal constrictor (constrictor pharyngis of Wiedersheim) is formed from cells

[1] The adult condition of the dorsal larynx and its musculature has been fully described by Wiedersheim.

given off from the cœlomic epithelium ; it spreads upwards round the œsophagus and dorsal larynx, forming the constrictor laryngis, and subsequently, in $9\frac{1}{2}$ mm. embryos, spreads forward to the branchial region and becomes attached to the os pharyngeum superior (of van Wijhe, the Pharyngealplatte of Wiedersheim) forming the transversus dorsalis and first obliquus dorsalis. The dilatator laryngis is formed from the dorsal part of the œsophageal constrictor (Text-fig. 32). The development of the retractor and protractor laryngis is described on pp. 238 and 267.

The development of the dorsal larynx of Amia is similar to that of Lepidosteus. The forward extension of the œsophageal constrictor begins in $8\frac{1}{2}$ mm. embryos (Text-figs. 30, 31, 32) ; it forms the transversus anterior and posterior and first obliquus dorsalis (of Allis). In Salmo fario the transverse fibres become attached to the fifth cerato-branchial, the fourth pharyngo- and epi-branchial and the third pharyngobranchial.

The ventral larynx and musculature of Polypterus have been described by Wiedersheim, who says that the muscles consist of a dilatator and sphincter glottidis, the latter of which is continuous below with a muscle-sheet surrounding the lungs. As stated above, the dilatator is the transversus ventralis IV. The sphincter glottidis is continuous above with the constrictor of the œsophagus, which is not attached laterally to the trunk muscles.

The development of the ventral larynx of Ceratodus has been described by Kellicott, and the adult condition by Wiedersheim. It may be added that the posterior edge of transversus ventralis V underlies the lung, and that, though there is no dorso-laryngeus (Wiedersheim), the lateral edges of the constrictor of the œsophagus are attached to the lower ends of the trunk-myotomes (Text-fig. 49).

It was supposed by Gegenbaur, Wilder, Göppert, and Drüner, that the cartilagines laryngei of Amphibia were branchial bars, and that the laryngeal muscles were derivatives of branchial muscles. Wilder stated that the dorso-

laryngei s. dorso-tracheales were serially homologous with the levatores arcuum branchialinm (called by him " dorso-branchiales "), that the laryngei were homologous with the transversi ventrales (called by him " pharyngo-branchiales "), and that these muscles and the laryngeal cartilages belonged to the fifth branchial arch.

This theory of the nature of the laryngeal muscles was formed on the evidence of adult anatomy only, without knowledge of the method of development.

Wiedersheim stated that the fibro-cartilage present in association with the ventral larynx of Protopterus might be due to the remains of a sixth arch, " noch plausibler aber erscheint es mir die betreffenden Knorpel auf einen in der Raphé des pharyngealen Constrictors sich abspielenden Chondrificationsprocess, das heisst auf Muskelwirkung züruckzufuhren "; also that " a priori steht der Annahme gewiss nichts in der Wege das sich auch bei Amphibien die primitive Cartilago lateralis als eine Sehnenverknorpelung bilden kann ohne das dabei phylogenetische Beziehung zu den Kiemenbogen angenommen werden mussen."

In Necturus the larynx is formed as a median ventral pouch of the pharynx in the hinder part of the fourth branchial segment in 13 mm. embryos (Text-figs. 53, 54). The cells which form the constrictor of the œsophagus are budded off from a thickened portion of the splanchnic cœlomic epithelium, and spread upwards round it (Text-fig. 54). A similar production of splanchnic mesoblast from a thickened portion of splanchnic cœlomic epithelium takes place in the fourth branchial segment (Text-fig. 52), and the cells spread upwards round the developing larynx and pharynx. In $14\frac{1}{2}$ mm. embryos this splanchnic meso-derm spreads upwards on either side of the pharynx internal to the fourth levatores arcuum branchialium, and forms the Anlagen of the dorso-laryngei and of the pharyn-geal constrictor (Text-fig. 56). The splanchnic mesoderm ventral to the pharynx develops into the laryngei muscles, and, next the larynx, the laryngeal cartilages.

A similar development of the laryngeal muscles takes place in Triton and in Rana.

If the method of development of the laryngeal muscles be compared with that of the branchial muscles it is seen that they are very different. The branchial muscles are developed from the branchial myotomes, the laryngeal muscles are differentiations of an œsophageal or pharyngeal constrictor, which is formed from cells given off by the cœlomic epithelum. In Polypterus and Ceratodus the larynx is developed just behind the branchial region, in Amphibia in the last, i. e. fourth branchial, segment. In Polypterus the œsophageal constrictor is not attached to the trunk-myotomes; in Ceratodus it is attached, though no dorso-laryngei are developed; in Amphibia dorso-laryngei are developed. In Ceratodus there are no intrinsic laryngeal muscles; in Polypterus there is a sphincter glottidis, which remains in continuity with the constrictor of the œsophagus; in Amphibia there are laryngei or a sphincter laryngis, which is not continuous with the constrictor of the pharynx. In Polypterus and Ceratodus there are no skeletal structures; in Amphibia laryngeal cartilages are developed—later than the branchial bars and ventral, not lateral to the pharynx. These similarities and differences suggest that the conditions found in Polypterus and Ceratodus preserve stages in the phylogenetic development of the laryngeal structures of Amphibia. They tend to confirm the theory of Wiedersheim. The relations of the transversus ventralis of the last branchial segment (fourth in Polypterus and Amphibia, fifth in Ceratodus) to the laryngeal structures have been described above.

In 5 mm. embryos of Chrysemys the opening of the larynx is in the fourth branchial segment; the cœlomic epithelum in the third and fourth branchial segments is thickened and proliferating mesoblast cells, which surround the pharynx and developing larynx. In 8 mm. embryos the opening of the larynx is in the third and fourth branchial segments; in the fourth a constrictor pharyngis is formed from the splanchnic mesoblast; in the third and fourth the Anlagen of

the sphincter laryngis and dilatator laryngis (Text-fig. 69) are formed, the latter having a vertical position and passing up outside the vagus. The dilatator has lost this position in 15 mm. embryos, and its hind end is attached to the cricoid. This supports the theory of Göppert that the dilatator laryngis of Sauropsida is the homologue of the dorso-laryngeus, and the sphincter the homologue of the sphincter and laryngei of Amphibia.

In 3 mm. embryos of the rabbit, cells are proliferated from the cœlomic epithelium in the three branchial segments (Text-fig. 80) ; they spread upwards internal to the branchial aortic arches. In 5 mm. embryos they have spread a little round the pharynx in the second and third branchial segments (Text-figs. 85, 86), but in the first they exist only lateral to it. In 6 mm. embryos the splanchnic mesoblast forms a continuous sheet dorsal to the pharynx in the second and third segments, but in the first it is still only lateral to it. In 7 mm. embryos it is present there also, more probably as a result of forward extension from the second branchial segment than of upward extension in the first segment. This continuous splanchnic mesoderm sheet is continuous behind with that round the œsophagus (Text-fig. 90), which is formed in a similar way.

The stylo-pharyngeus is formed in the splanchnic mesoblast of the first branchial segment ; it is first visible in $7\frac{1}{2}$ mm. embryos and gains an attachment to the hyoid bar (Text-fig. 93). The pharyngeal constrictor is also formed in the three branchial segments, though, perhaps, vide supra, derived from cells of the second and third segments only. The Anlage of the laryngeal muscles is also visible in $7\frac{1}{2}$ mm. embryos in the third branchial segment. The later development of the laryngeal muscles, in man, has been traced by Frazer, who says that they are developed in the third branchial segment from the ventral part of the layer of cells round the pharynx and larynx ; of this laryngeal portion " the formation of the arytenoid seems to convert the dorsal hinder part into the crico-arytenoideus posticus, the upper

part into the arytenoidens, and the ventral part into the thyro-arytenoidens and lateral crico-arytenoid." According to Göppert, the crico-arytenoidens posticus is the homologue of the dorso-laryngeus of Amphibia, the other intrinsic muscles representing the sphincter and laryngei dorsalis and ventralis of Amphibia.

TEXT-FIG. 72.
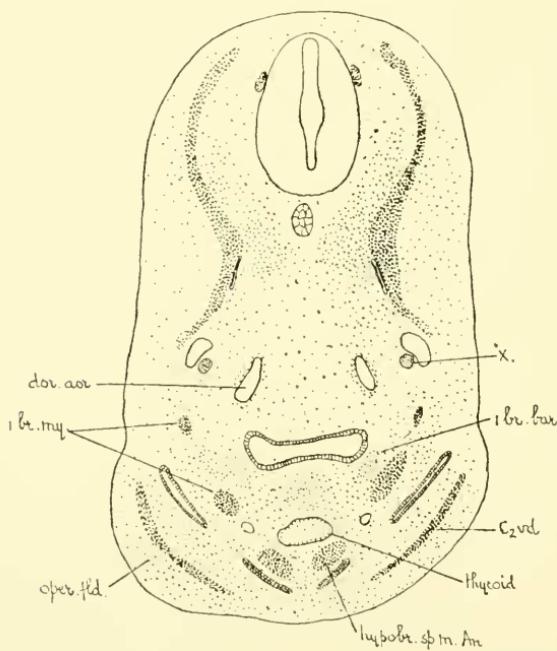
72.

Text-figs. 72, 73.—Gallus, embryo four days. Text-fig. 72 through the first branchial. Text-fig. 73 through the second branchial segment.

Frazer states that in man the thyroid cartilage is developed solely in the second branchial segment, i. e. it is the second branchial bar only, whereas in Echidna (Göppert) a third branchial bar is also formed.

The crico-thyroideus, according to Frazer, is developed

from the second branchial pharyngeal constrictor; this confirms the opinion of Fürbringer.

The pharyngeal musculature extends forwards into the mandibular segment in 13 mm. embryos (Text-fig. 94) ; in 14 mm. embryos the anterior end becomes separated, forming the tensor palati, and in 16 mm. embryos the next succeeding portion forms the levator palati.

TEXT-FIG. 73.
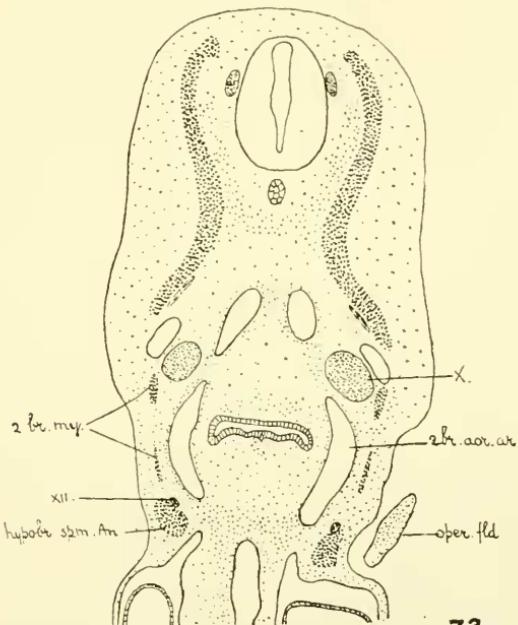
73.

According to Futamura, as stated above, the Anlage of the palatal muscles of man is at first one with that of the tensor tympani, and is derived from the platysma faciei. I have failed in verifying this in the rabbit; the platysma faciei in that animal remains superficial, and the Anlage of the palatal muscles when first visible was quite distinct from that of the tensor tympani, which is cut off from the inner limb of mandibular myotome.

These phenomena afford an explanation of the innervation of the palatal muscles by the XIth medullary.

MUSCLES DERIVED FROM TRUNK-MYOTOMES PASSING TO THE UPPER ENDS OF THE BRANCHIAL BARS.

Vetter described a subspinalis and interarcuales muscles in
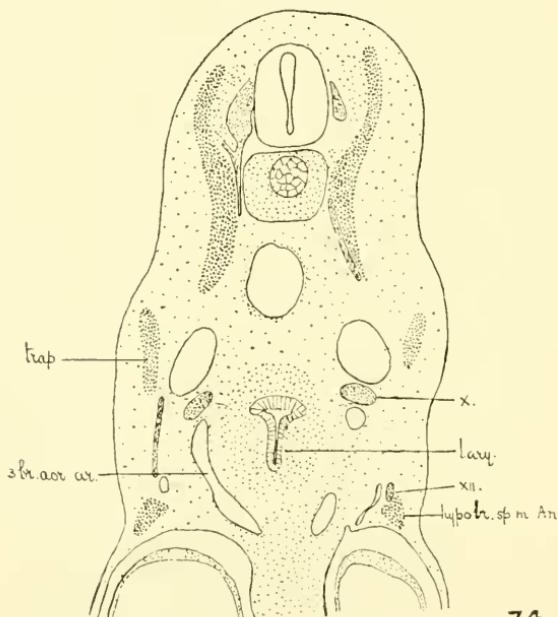
TEXT-FIG. 74.

Gallus, embryo 4½ days, transverse section.

Selachii. Fürbringer subsequently showed that the subspinalis and upper interarcuales (which he re-named " interbasales "), were innervated by the spino-occipital nerves, and he classed them together as "epibranchial spinal muscles." The lower interarcuales (second and third interarcuales of Vetter), he called " arcuales dorsales."

Observation of the development of these muscles confirms Fürbringer's theory of their nature. The subspinalis and

¹ Beevor and Horsley.

first, second, and third[1] interbasales of Scyllium are developed
in 23 mm. embryos from the first, second, third, and fourth
spinal myotomes (Text-figs. 12, 13, 14), by growths from their
ventral edges internal to the ganglia of the ninth and tenth
nerves.

A retractor arcuum branchialium dorsalis is found in
some Teleosteii (Vetter), e. g. Perca and Cyprinus, in Amia
(Allis, Wiedersheim[2]), and in Lepidosteus (Wiedersheim[2]),
but is not present in Polypterus (Pollard), or in Salmo fario.
In Amia the muscle, which is inserted into the third infra-
pharyngo-branchial, arises according to Allis from the third
and fourth, according to Wiedersheim from the seventh and
eighth, vertebral bodies. In Lepidosteus the muscle is
inserted into the third infrapharyngo-branchial, and arises
from the lateral surface of the third and fourth vertebral
bodies (Wiedersheim). The retractor was supposed by Allis
and by Wiedersheim to belong to the system of the levatores
arcuum branchialium.

The muscle is developed in Amia from downgrowths from
the lower surface and lower part of the internal surface of the
sixth to thirteenth trunk-myotomes in $8\frac{1}{2}$ mm. embryos (Text-
fig. 33); these downgrowths form a longitudinal muscle, the
anterior end of which grows forward to the third bar. Its
development in Lepidosteus is similar, taking place, in 12 mm.
embryos, from the third to ninth trunk-myotomes.

HYPOBRANCHIAL SPINAL MUSCLES.[3]

In Scyllium, van Wijhe stated that the coraco-hyoideus
was developed from ventral prolongations " sowohl des hin-
stersten Kopfmyotomes als die der vorderen Rumpfmyotome,"
and that the coraco-branchiales and coraco-mandibularis
were formed from the walls of the " unpaaren vorderen

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[1] The third interbasalis, developed in the embryo, is not described in
the adult by Fürbringer.

[2] Retractor laryngis of Wiedersheim.

[3] This name is used in the sense stated above.

Verlängerung des Pericardiums." Neal, in Squalus acanthias, found that the Anlage of the hypoglossus musculature was formed from the fourth to the eighth post-otic myotomes by buds which separate and come to lie ventral to the branchial basket; they do not fuse into a common cell mass, but show their primary metamerism, the bud from the fourth myotome coming to lie between the hyoid and mandibular cartilages and forming "in part the Anlage of the proper tongue muscles," whilst "the four following myotomic buds come to lie between the hyoid and procoracoid."

I find that in Scyllium the initial stages of the development of the coraco-mandibularis and coraco-hyoideus are similar to those of Squalus acanthias, as stated by Neal. This stage is completed in 16 mm. embryos, and is immediately followed by one (17 mm.), in which the hind end of the primitive genio-hyoideus, which does not become affixed to the hyoid bar, grows backwards along the median edge of the coraco-hyoideus towards the shoulder-girdle—forming the coraco-mandibularis (Text-figs. 11, 12, 13).

The coraco-hyoideus of Salmo salar (Harrison) is developed from ventral downgrowths of the second, third, and fourth trunk myotomes, which bend round the pharyngeal region, and form a longitudinal column, the anterior edge of which extends forwards to the hyoid bar. A similar development of the hypobranchial spinal muscles takes place in Acipenser, Lepidosteus, Amia, and Salmo, occurring in 8 mm., 8 mm., 7 mm., and 5 mm. embryos respectively, and in each case from the second, third, and fourth trunk myotomes. In Salmo fario and in Lepidosteus the forward growth of the anterior end reaches the hyoid bar only, so that only a coraco-hyoid is formed. In Acipenser and Amia it extends further, to the symphysis, reaching this in $8\frac{1}{2}$ mm. embryos of Acipenser (Text-figs. 21, 22), and in 8 mm. embryos in Amia. The long column then divides at the level of the hyoid bar into an anterior and a posterior group—the genio-hyoid[1]

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[1] Branchio-mandibularis of Vetter and Allis.

and coraco-hyoid.[1] The posterior end of the genio-hyoid grows backwards (Text-figs. 28, 29, 30), and becomes attached, in Acipenser to the third hypobranchial, and in Amia by two tendons, to the second and third hypobranchials and to a median aponeurosis between the two coraco-hyoidei (Y-shaped tendon of Allis).

In Polypterus,? species, Pollard described the hypobranchial spinal muscles as consisting of a branchio-mandibularis s. genio-hyoideus extending from the symphysis of the lower jaw to the first basi-branchial, and of a coraco-hyoideus which had an additional tendon attached to the first cerato-branchial. Fürbringer described the muscles as consisting of a coraco-mandibularis extending from the symphysis to the shoulder-girdle, and of a coraco-hyoideus.

In Polypterus senegalus (Text-figs. 35, 36, 37), the muscles consist of a genio-hyoideus and a coraco-hyoideus ; the former extends from the symphysis backwards to the level of the third branchial bar, where it ends by being attached to the third cerato-branchial and by a tendon which passes downwards and is attached to a little median ossicle lying between the two coraco-hyoidei. The coraco-hyoideus extends from the cerato-hyal backwards to the shoulder-girdle, and has no tendon passing to the first cerato-branchial.

Greil stated that the "hypobranchial musculature" of Ceratodus was developed from ventral downgrowths of the third and fourth myotomes. He apparently included the coraco-branchiales as well as the coraco-mandibularis and coraco-hyoideus under this head, as the first-named were not described as developing in the branchial region. It has been stated above (p. 234) that the coraco-branchiales are developed from the lower ends of the branchial myotomes. The hypobranchial spinal muscle Anlage spreads forwards (Text-fig. 39) reaching the anterior extremity of Meckel's cartilage in stage 43. The portion in front of the hyoid bar separates

[1] Main portion of coraco-arcualis anterior (Vetter) in Acipenser ; hyopectoralis (McMurrich), sterno-hyoideus (Allis) in Amia ; the term used above is that of Fürbringer.

from that behind, and its hind end grows backwards below
the coraco-hyoideus (Text-figs. 45, 46, 47) to the shoulder-
girdle, forming the coraco-mandibularis. The portion behind
the hyoid bar forms the coraco-hyoidens; in stage 63 it is
partially separated into the coraco-hyoidens and abdomino-
hyoidens of the adult, of which the latter is continuous with
the trunk muscles behind the shoulder-girdle.

In Necturus (Miss Platt) the hypobranchial spinal muscles
are developed from ventral downgrowths of the third, fourth,
and fifth post-otic somites, joined by a few scattered cells
from the second somite; the genio-hyoidens is formed from
the third, the sterno-hyoidens from the fourth and fifth.

In Triton there is a similar development from the third,
fourth, and fifth trunk myotomes in 6½ mm. embryos.

The hypobranchial spinal muscles of Rana are developed
from downgrowths of the first and second trunk myotomes
in 6 mm. embryos (Text-fig. 57), which bend round the bran-
chial region, forming a longitudinal column which reaches
the inferior labial cartilage in 8 mm. embryos. It divides
opposite the third branchial bar into genio-hyoid and sterno-
hyoid.[1] The front end of the former is attached to the
inferior labial cartilage (Text-figs. 60, 62), and its hind end to
the hypobranchial plate as far back as the antero-posterior level
of the third branchial bar. In 12 mm. embryos the internal
portion of the genio-hyoid is proliferated from the median edge
of the original muscle (Text-fig. 59). At metamorphosis the
inferior labial cartilage forms the anterior end of the lower
jaw, and the muscle so retains its primitive attachments. The
front end of the sterno-hyoid becomes attached to the third
cerato-branchial, and the muscle extends back to the dia-
phragm. Towards metamorphosis the shoulder-girdle is
developed and the sterno-hyoid becomes attached to it, and
a little later the omo-hyoid is separated from its external
edge.

In Alytes, Bufo lentiginosus and Pelobates there is no

[1] Genio-hypobranchialis and diaphragmato-branchialis medialis of
Schultze.

proliferation of an internal portion of the genio-hyoid ; otherwise the condition in the larvæ is the same. In Alytes the hind end of the genio-hyoid is attached to the third cerato-branchial.

In the rabbit the hypobranchial spinal muscles are formed from downgrowths of the first three trunk myotomes in 4 mm. embryos (Text-fig. 82). These have separated in $4\frac{1}{4}$ mm. embryos, and form a longitudinal column which extends forwards dorsal to the interhyoideus and intermandibularis, reaching the anterior extremity of Meckel's cartilage in 8 mm. embryos, and backwards, reaching the area of the anterior limb in 7 mm. embryos. In 13 mm. embryos it has divided into genio-hyoid and (primitive) sterno-hyoid, the adjacent ends of which are attached to the first branchial bar. In 17 mm. embryos the primitive sterno-hyoid has divided into the sterno-hyoid, sterno-thyroid, thyrohyoid, and omo-hyoid. The first trunk myotome, from which the most anterior of the downgrowths above mentioned takes place, atrophies in $7\frac{1}{2}$ mm. embryos, the second and third in 9 mm. embryos.

The Homologies of the Hypobranchial Spinal Muscles.—In Amphibia, Sauropsida, and rabbit, the Anlage of the hypobranchial spinal muscles divides into anterior and posterior portions—the genio-hyoid and sterno-hyoid. The former extends from the symphysis of the lower jaws to the basi-branchial or some branchial bar, the latter extending thence to the shoulder-girdle or sternum. The division takes place in the neighbourhood of the first branchial bar in Urodela, Sauropsida, and rabbit; in Anuran larvæ it is at the level of the third branchial bar.

In Scyllium, Teleostomi, and Ceratodus, a similar division of the Anlage of the hypobranchial spinal muscles takes place at the level of the hyoid bar; the hind end of the anterior portion, which does not gain any temporary insertion to the hyoid bar, then grows backwards ventral or ventro-lateral to the posterior portion (coraco-hyoideus) and becomes attached to the first (Polypterus, ? species, described by Pollard), or to the second and third (Amia), or third (Polypterus sene-

galus, Acipenser) branchial bar, or to the shoulder-girdle, forming a coraco-mandibularis (Scyllium, Ceratodus, Polypterus? species, described by Fürbringer).

The anterior attachment of the genio-hyoid and coraco-mandibularis is to the front end of Meckel's cartilage except in Anuran larvæ, where it is to the inferior labial cartilage. In Acanthias, where there is an inferior labial cartilage (Gaupp), the coraco-mandibularis is not attached to this but to Meckel's cartilage. In Callorrhynchus (Fürbringer) there is a coraco-præmandibularis developed, attached anteriorly to the inferior labial cartilage.

Fürbringer homologised the genio-hyoidens with the coraco-mandibularis of Selachii, and supposed that the former was derived from the latter, by giving up its attachment to the shoulder-girdle, and gaining a new one to (more rostally lying) portions of the hyobranchial skeleton. Such a deduction was a legitimate one from the evidence of adult anatomy only, though the alternative was possible, and the embryological history of the muscles shows that it is this alternative which occurs; the condition in Teleostomi, Elasmobranchs, and Ceratodus is a secondary one.

The method of development of the hypobranchial spinal muscles in Scyllium lends additional interest to, and receives corroboration from, some anatomical facts described by Vetter and Fürbringer. The degree of backward extension of the coraco-mandibularis towards the shoulder-girdle varies, even amongst the Selachii. Thus in Heptanchus and Scyllium it does not reach the coracoid, whereas in Læmargus and Prionodon it does. Further, the coraco-mandibularis is not crossed by tendinous inscriptions, in this forming a marked contrast to the coraco-hyoideus, alongside of which it lies. The only possible exception to this among the forms depicted by Fürbringer is Cestrastion, and this is probably an apparent one only; it is possible that the tendinous inscription really separates the coraco-hyoideus from the coraco-manibularis, which only reaches the coracoid by its median edge. Similarly, according to Fürbringer, there are three tendinous

inscriptions in the cerato-hyoideus of Ceratodus, whilst there is only one doubtful one in the coraco-mandibularis;[1] in Protopterus there are two in the coraco-hyoideus, none in

TEXT-FIG. 75.
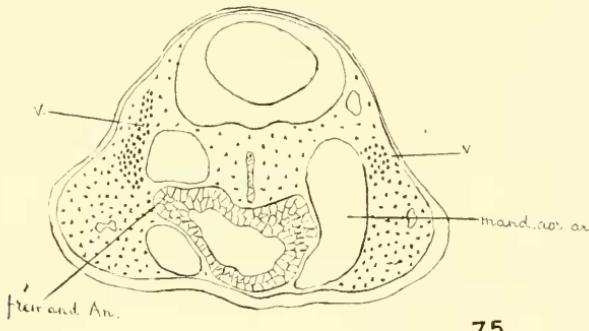
75.

TEXT-FIG. 76.
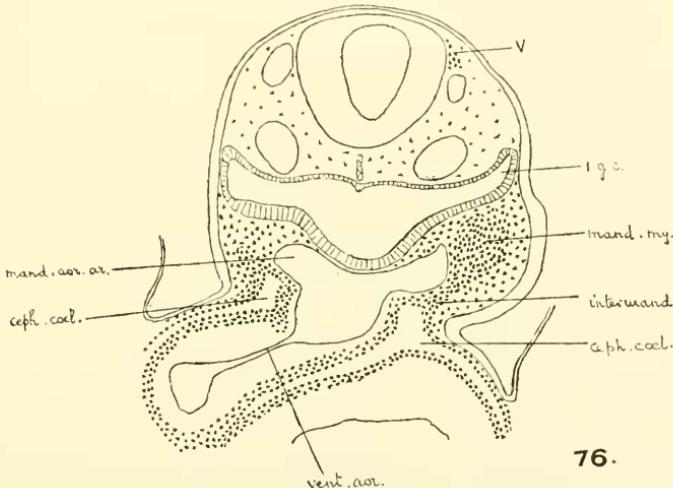
76.

Text-figs. 75–77.—Rabbit, embryo 3 mm. Text-fig. 75 is through the premandibular Anlage, Text-fig. 76 through the mandibular segment, Text-fig. 77 through the hyoid segment.

the coraco-mandibularis; in Polypterus ? species there are two in the coraco-hyoideus, none in the coraco-mandibularis.

[1] It was not apparent in stage 63 (vide Text-fig. 45).

Again, there are two inscriptions in the coraco-hyoid of Amia (Allis), and Acipenser (Vetter), none in the genio-hyoid.

The non-development of a genio-hyoid, even as an atrophy-ing Anlage, in Lepidosteus and Salmo would appear, on comparison with other forms, to be a secondary condition.

The developmental history of the hypobranchial spinal muscles suggests that their Anlage was primitively an undivided column, extending forward to the symphysis of

TEXT-FIG. 77.
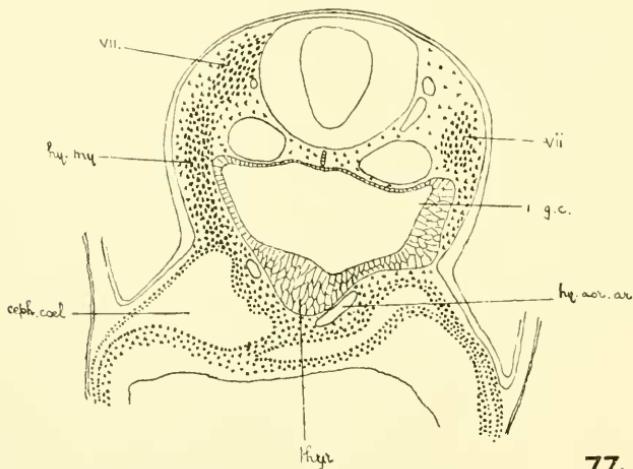
77.

the jaws, an anterior prolongation of the rectus system of the trunk into the head segments. This divided into genio-hyoid and coraco-hyoid. In fishes the genio-hyoid secon-darily extended backwards, overlapping the coraco-hyoid in varying degrees.

The Anlage of the hypobranchial spinal muscles is formed from downgrowths of several—two or more—trunk myotomes, that from the foremost myotome taking part in its formation extending furthest forward, that from the next succeeding it, and so on. There is a certain correlation between the number of trunk myotomes taking part in the

formation of the hypobranchial spinal muscles and the number of trunk-segments included in the skull (vide table, p. 299). In general, the less the number of trunk-segments included in the skull, the greater tendency there is for the most anterior trunk myotomes to take part in the formation of the hypobranchial spinal muscles, and the less the number of anterior trunk myotomes atrophying without taking part in their formation. The table also shows that the hypobranchial spinal muscles are derived from a variable number of trunk myotomes. The number varies from two (Rana) to five (Scyllium). Derivation from the smallest number is probably the most primitive condition. The number does not vary with that of the trunk-segments included in the skull, nor with the number of head-segments.

LINGUAL MUSCLES.

The researches of Gegenbaur and Kallius in Salamandrina have shown that the genio-glossus is developed from the genio-hyoideus and the sterno-glossus from the sterno-hyoideus ; the former ends between the lingual glands which form the fore part of the tongue, and is " also ein Drüsen Muskel " (Gegenbaur) ; the latter becomes attached to a plate of dense connective tissue which probably develops at the site of fusion of the primitive tongue with the glandular portion. Kallius has also shown that in the Anura the genio- and hyo-glossus are developed from the genio-hyoid. The genio-glossus grows towards the subsequently glandular, precopular field, and later, the hyo-glossus fibres cross those of the genio-glossus.

To this may be added that in Rana the genio- and hyo-glossus are developed from the inner division of the genio-hyoid, which (vide p. 270) is proliferated from the inner side of the primitive muscle.

In 27 mm. larvæ of Alytes the genio-glossus ends free beneath the mucous membrane of the precopular field, and the hyo-glossus passes forward at first below and then lateral

to the long forward projecting basihyal (Text-fig. 63), and is attached to it near its anterior end. In larvæ of Bufo, Rana, and Pelobates the hyo-glossus is not attached to the rudimentary basihyal.

The development of the lingual muscles of Lacerta muralis has also been investigated by Kallins. The development of the lingual muscles in other groups of Sauropsida (loc. cit.) showed that the primitive condition of the lingual muscles is a genio- and hyo-glossus, both developed from
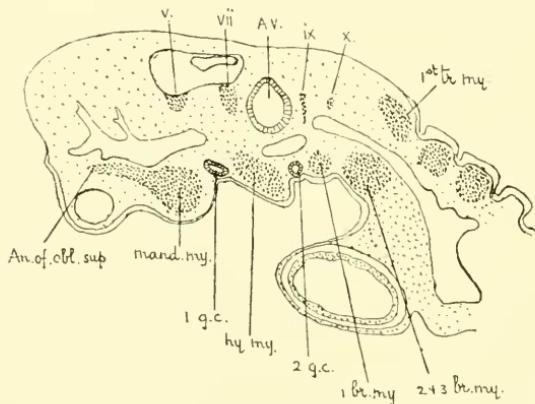
Rabbit, embryo 3¼ mm., longitudinal vertical section.

the genio-hyoid, attached to the long basihyal, the former to its front end, the latter to its side; and that extension into the tongue is a secondary phenomenon.

The condition of the hyo-glossus of Alytes is of interest when considered in relation to that of the lingual muscles of Sauropsida. Gegenbaur was of opinion that "die Muskularisirung scheint vorwiegend im Dienste der Drusen zu stehen." An alternative hypothesis suggested by the condition in Alytes larvæ would be that the condition in Sauropsida is the primary one, and that their functions as glandular muscles in Amphibia is correlated with the absence (e.g.
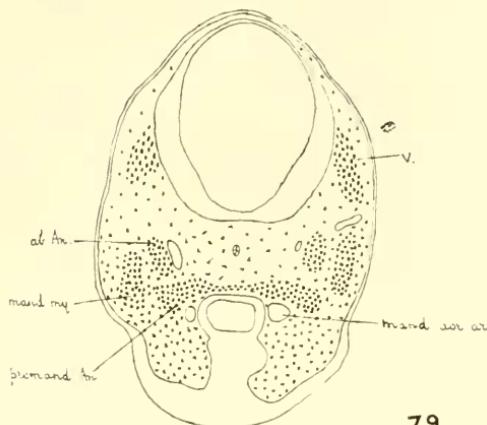
TEXT-FIG. 79.

Rabbit embryo 3¼ mm. The upper part of the section is posterior to the lower.
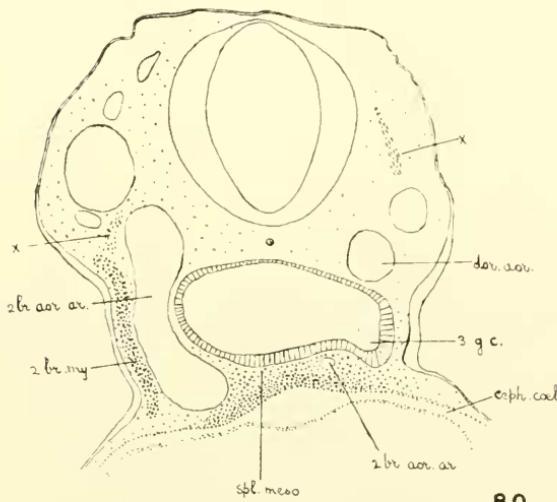
TEXT-FIG. 80.

Rabbit, embryo 3¼ mm. The right side of the section is a little anterior to the left, which passes through the second branchial myotome.

Triton) or rudimentary condition (e.g. Rana, Pelobates, Bufo) of the basihyal.

In the rabbit the Anlagen of the lingual muscles are formed from the anterior part of the Anlage of the hypobranchial spinal muscles, i.e. from the future genio-hyoid, in 9 mm. embryos, that of the genio-glossus and lingualis by upward growth, that of the hyo-glossus and stylo-glossus by an out-

TEXT-FIG. 81.
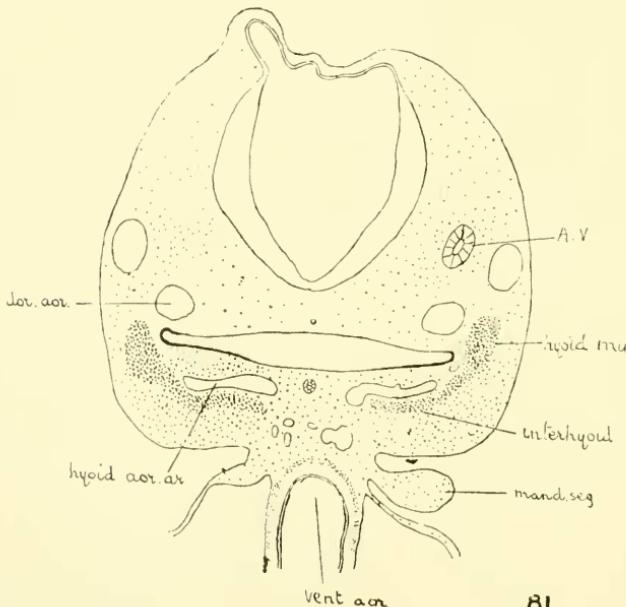
Text-figs. 81–83.—Rabbit, embryo 4 mm. Text-fig. 81 is through the hyoid segment. Text-fig. 82 through the fourth gill-cleft. Text-fig. 83 through the third branchial gill-cleft.

growth directed upwards and laterally (Text-fig. 91). In 13 mm. embryos these muscles have separated from the genio-hyoid, and become distinct (Text-figs. 94, 95).

SOME PHYLOGENETIC CONSIDERATIONS.

The probable phylogenetic relationships of the various Vertebrate groups are determined by the total morphological

TEXT-FIG. 82.

82.

TEXT-FIG. 83.

83.

20
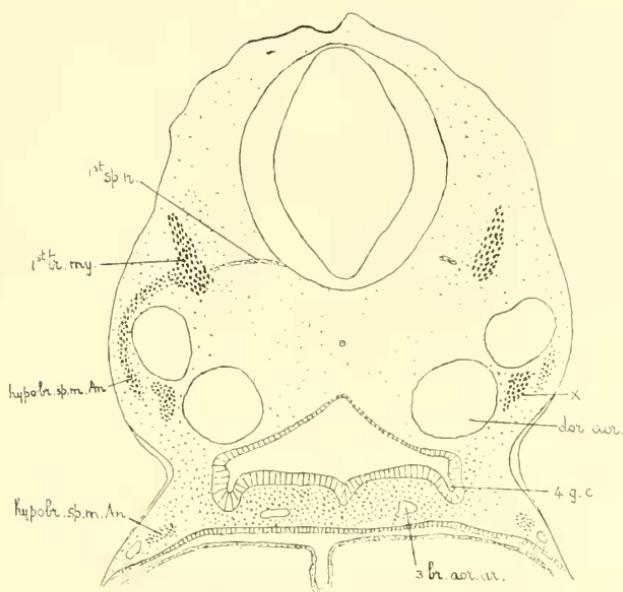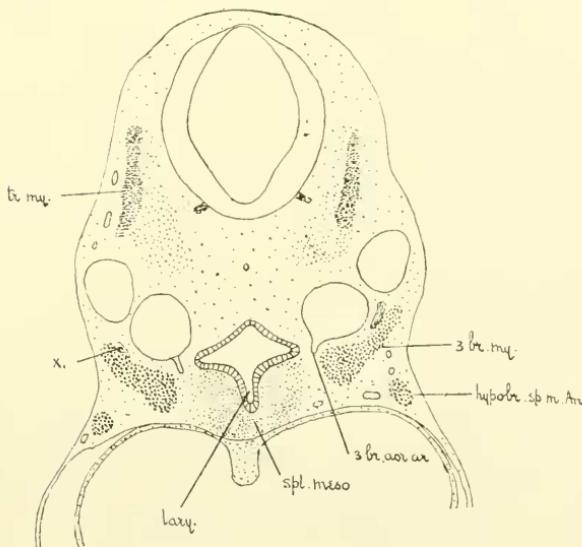
evidence available. The cranial muscles form one item only of such evidence, but it is of interest to inquire how far their morphology falls in with generally received opinion, and in what direction it points in cases where opinions vary.

Such an inquiry is beset by the difficulties which arise from—(A) secondary innervation of muscles; (B) development of similar changes in various groups; (C) atrophy, and non-development of muscles.

(A) Comparison of the development and innervation of the cranial muscles shows that although, in general, a muscle is innervated by the nerve corresponding to its segment of origin, yet this is not invariably the case. Thus:

(1) The posterior part of the intermandibularis of Triton is innervated by the VIIth (Drüner).[1]

(2) The intermandibularis of Selachians is, in part, e.g. Scyllium (Vetter), or wholly, e.g. Acanthias (Vetter), innervated by the VIIth.

(3) The intermandibularis anterior and posterior (the latter called "inferior genio-hyoid" by Allis) of Amia are innervated by both the Vth and VIIth (Allis).

(4) The hyo-maxillaris of Teleostomi, developed in the hyoid segment, is in some, e.g. Menidia (Herrick), wholly innervated by the VIIth; whereas in others, e.g. Esox (Vetter), Salmo, its hinder part is innervated by the VIIth and its fore part by the Vth; and in Amia (Allis) it is innervated by the Vth and VIIth.

(5) The anterior digastric of man, pig (Futamura), and rabbit, developed in the hyoid segment, is innervated by the Vth.

(6) The cerato-hyoideus externus of Urodela, developed in the hyoid segment, is innervated either by the VIIth, e.g. Necturus (Miss Platt), or by the IXth, e.g. Triton (Drüner).

(7) The interarcuales ventrales of Urodela are innervated both by the nerves corresponding to their segments of origin and also by those of the next anterior segments (Drüner).

(8) In some Teleostomi, e.g. Polypterus senegalus,

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[1] Roman numerals denote cranial nerves.

Esox (Vetter), Menidia (Herrick), Amia (Allis), Lepidosteus, the only coraco-branchialis present, developed from the most posterior branchial segment (fourth or fifth), is innervated by the Xth ; whereas in others, e. g. Amieurus (Wright), Salmo (Harrison), it is innervated by the spino-occipital nerves.

(9) The coraco-branchiales of Acipenser, Ceratodus, and Scyllium, developed in branchial segments, are innervated by spino-occipital nerves (Vetter, Fürbringer). The spino-occipital nerves also innervate the four coraco-branchiales of Polypterus (?) species, described by Fürbringer.

(10) The capito-dorso-clavicularis of Lacerta agilis, developed from the primitive trapezius, i. e. from branchial segments, is innervated by spinal nerves (Fürbringer).

(11) The cucullaris, i. e. trapezius, of Gallus, developed from branchial segments, is innervated both by the XIth and by spinal nerves (Fürbringer).

(12) The trapezius and sterno-mastoid of the rabbit, developed from branchial segments, is innervated both by the XIth and by spinal nerves.

(13) The retractor arcuum branchialium dorsalis of Amia and Lepidosteus, developed from trunk myotomes, is innervated by the Xth (Allis, Wiedersheim).

(14) The hinder part of the hypobranchial spinal muscles of the rabbit, which are developed from the first three spinal myotomes, are innervated by more posterior spinal nerves.

(15) The interarcualis ventralis I, i. e. branchio-hyoideus or branchio-mandibularis of Sauropsida, is innervated by the XIIth.

Fürbringer held that " Die Innervirung der Muskeln durch bestimmte Nerven ist das wichstigte Moment fur die Vergleichung." In criticism of this theory, Cunningham gave instances from the myology of the trunk and limbs in which this criterion failed, and concluded that the nerve supply is " not an infallible guide " for determination of the homology of a muscle. The above-cited observations show that developmental phenomena should be taken into consideration.

The first fourteen of the phenomena recorded appear to be referable to a common cause; if a muscle spreads into one or more neighbouring segments, that portion tends to be innervated by the corresponding nerve or nerves. The backward extension of the origin of the XIth appears to be referable to the same cause.

It is not yet known what happens within the central nervous system—whether there is a corresponding migration of motor neuroblasts or whether new ones are locally formed.

The cause of the phenomenon cited under (15) above is much more obscure. The muscle is the interarcualis ventralis of the first branchial segment, and is homologous with the similarly developed muscle of Amphibia, some Teleostomi, and some Mammalia, and yet, unlike them, it is innervated by spino-occipital nerves and not by the IXth, just as if it were a coraco-branchialis I.

(B) The possibility of the independent development of similar secondary changes in the various groups arises in the case of the hypobranchial spinal muscles, the hypobranchial cranial muscles, the levatores arcuum branchialium, and trapezius, the hyoid bar and related muscles, the adductor mandibulae.

In Ceratodus and in Scyllium the hind end of the genio-hyoid secondarily extends backwards to the shoulder-girdle. The question arises whether this feature is inherited from a common ancestor or whether it has been independently acquired. In favour of the second view are the facts that within the group of the Teleostomi all conditions exist between that of a genio-hyoid which has slightly extended backwards and a coraco-mandibularis.

A similar question arises in regard to the formation of coraco-branchiales in Ceratodus and Scyllium. Again, within the group of the Teleostomi all variations exist between interarcuales ventrales and their homologues, coraco-branchiales.

These secondary modifications in the hypobranchial-spinal and hypobranchial-cranial muscles appear to be morphological expressions of an increased need of tying the

mandibulo-hyo-branchial skeleton to the shoulder-girdle,
and the change of function of the latter group of muscles to
one similar to that of the former tends to bring about a
secondary innervation from spinal nerves.

A similar question arises in connection with the presence
and absence of levatores arcuum branchialium. It has been
suggested above that their absence and the related method
of formation of the trapezius are secondary phenomena
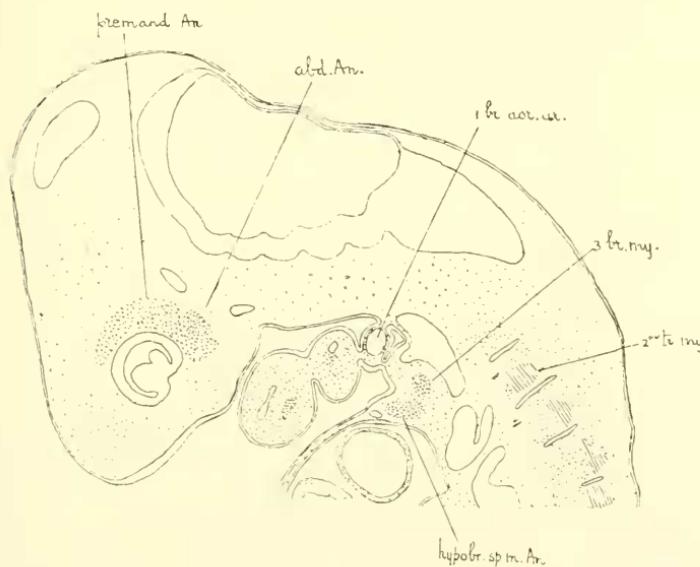
TEXT-FIG. 84.

Rabbit, embryo 4 mm., longitudinal vertical section.

(p. 257). If so, it is possible that this has been indepen-
dently acquired in Scyllium, Sauropsida, and rabbit.

In Scyllium and the Teleostomi a stage of development
occurs in which there is a short hyoid bar like that of
Amphibia with a levator hyoidei, which is succeeded by one
in which the bar extends up to the periotic capsule. The
relationship of the muscles and of the facial nerve to the
later formed portion of the bar are so different in Scyllium

and Teleostomi that possibly the only common feature is the above-mentioned first stage. In Ceratodus, Sauropsida, and rabbit the hyoid myotome is external to the upper part of the hyoid bar, as in Scyllium.

In Sauropsida and certain Teleostomi the adductor mandibulæ divides into internal and external portions, but in Teleostomi there is no uniform upgrowth of the external

TEXT-FIG. 85.
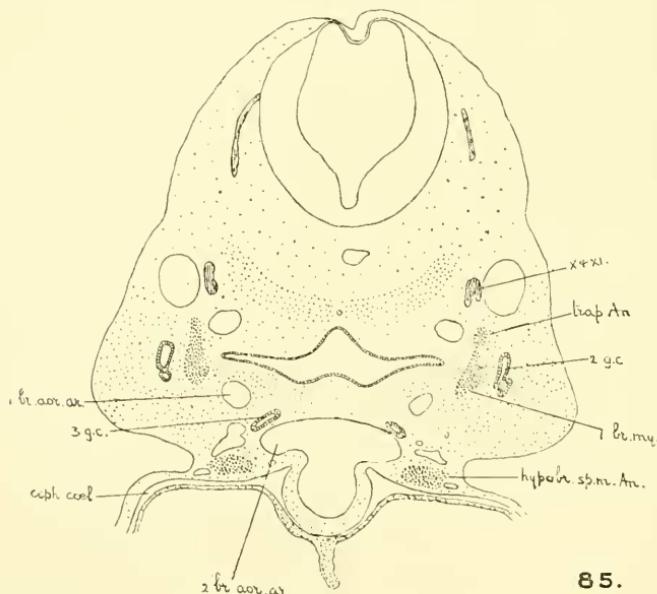
85.

Text-figs. 85–87.—Rabbit, embryo 5 mm. ; Text-fig. 85 is through the first branchial segment. Text-fig. 86 through the third branchial segment. Text-fig. 87 just behind this.

portion to the skull as in Sauropsida. Both division and upgrowth have been independent occurrences in these two phyla.

c. Amongst the animals investigated there are but few in which muscle-Anlagen are developed and then atrophy. The Mm. marginales and interarcuales ventrales of the larva of Rana, certain muscles of metamorphosing Urodela described by Drüner, the levator maxillæ superioris of Chelone and

TEXT-FIG. 86.

86.
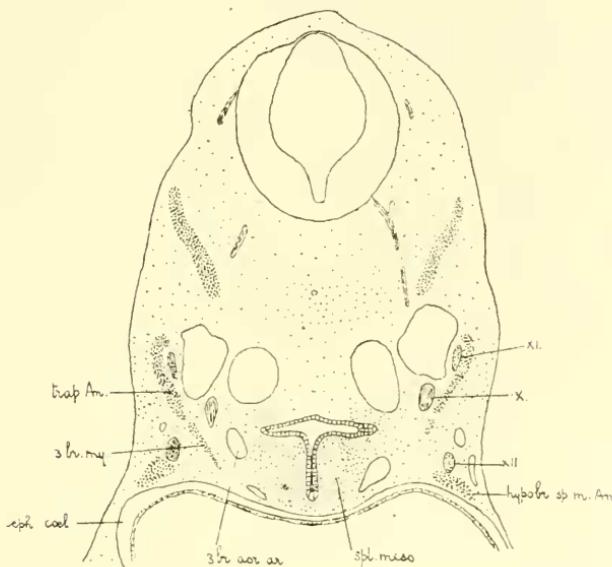
TEXT-FIG. 87.
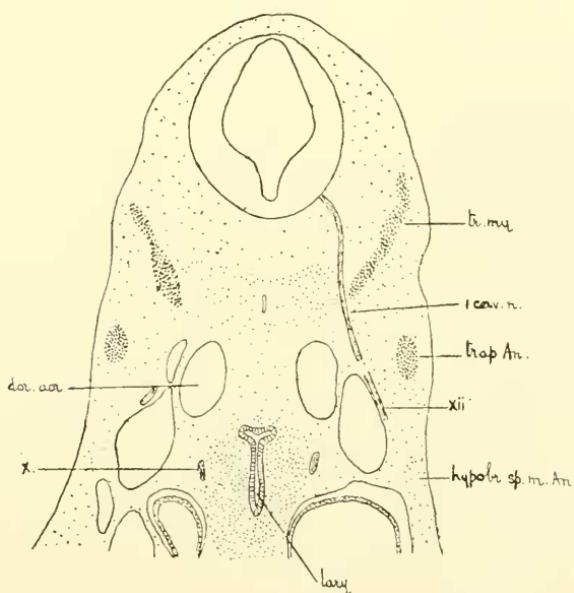
87.

Alligator, and the genio-hyoid of Gallus, were the only ones found. Otherwise if a muscle is not present in the adult it is not formed during development.

There are certain instances in which comparative evidence suggests that ancestors probably possessed muscles which are now no longer developed, even as Anlagen. Such are the genio-hyoid of Lepidosteus and Salmo, certain Mm. transversi ventrales in Amphibia and Teleostomi, the first two obliqui ventrales in Polypterus senegalus, the hyo-maxillaris in Selachii and Sauropsida, the levatores arcuum branchialium in Selachii, Sauropsida, and Mammalia.

Consideration of the changes which take place in the Anlagen of the cranial muscles in the various Vertebrate groups suggests that the most important are those occurring in the myotome of the mandibular segment. In Amphibia and Ceratodus it does not, whilst in Teleostomi, Selachii, and Sauropsida it does divide into parts above and below the palato-pterygoid or pterygoid process of the quadrate. It has been stated above that the embryological phenomena support the view that the second condition has been derived from the first. In the rabbit the quadrate (incus) has no pterygoid process, and the myotome—as in Amphibia and Ceratodus—does not divide into upper and lower parts.

Changes take place in the Anuran tadpole, in the form of the palato-quadrate bar and in certain muscles in association with the development of a suctorial mouth, i.e. the backward elongation of the mandibular muscles, the development of a submentalis and mandibulo-labialis, the origin of the orbito-hyoideus, or of this and the suspensorio-hyoideus, and the partial origin of the first branchial levator from the palato-quadrate bar, the division of the hyo-maxillaris and attachment of one or two of its parts to the palato-quadrate bar. As the condition before these events takes place is very like that of an embryo of Ceratodus or an Urodelan, it would appear probable that the changes are secondary larval ones and not ancestral.[1]

[1] The difficult question as to the origin and nature of the larval

On the other hand, the existence of a hyo-maxillaris and of Mm. marginales, the insertion of the orbito-hyoideus or of this and the suspensorio-hyoideus to the cerato-hyal, and the origin of the trapezius from the skull, are primitive features which are not developed or soon modified in Urodelan development.

In the Urodela the insertion of the levator hyoidei is transferred, wholly or partially, from the hyoid bar to Meckel's cartillage early in development, and the hyo-maxillaris Anlage forms a ligament. The development of gill-muscles from Anlagen which are homologous with those which give rise to the Mm. marginales of Anuran larvæ and Ceratodus, and of a cerato-hyoideus externus, are features peculiar to Urodela.

Ceratodus resembles Selachii and some Teleostomi, and differs from Amphibia in the backward growth of the genio-hyoid to the shoulder-girdle, and in the formation of coraco-branchiales. Ceratodus resembles Selachii and Teleostoman embryos, and differs from Amphibia in the backward growth of both hyoid myotome and interhyoideus, resulting in the formation of a continuous dorso-ventral sheet, C_2vd, behind the hyoid bar. Ceratodus resembles Teleostomi and Amphibia, and differs from Selachii in the formation of levatores arcuum branchialium and in the development of the trapezius from a levator. Ceratodus resembles Amphibia, and differs from Selachii and Teleostomi in the non-division of the mandibular myotome into upper and lower portions. Ceratodus resembles Anuran larvæ in the simple condition of the Mm. marginales, and Urodela in the ligamentous condition of the hyo-maxillaris.

According to K. Fürbringer, "Wenn wir somit keine bestimmte Ordnung der Amphibia von den Dipnoern ableiten konnen, so ergiebt sich daraus kein Einwand gegen eine Abstammung von den Dipnoern über-

condition of the suctorial mouth and jaws in Anuran larvæ was discussed by Balfour and by Gaupp, though without reference to the muscles.

haupt. . . ." The development, however, in Ceratodus, of
a coraco-mandibularis, of coraco-branchiales, of a hyoman-
dibula, and of a dorso-ventral sheet C_2vd behind the hyoid
bar, are all secondary to more primitive conditions present in
Amphibia.

Goodrich was of opinion that "the Dipnoi are probably a
specialised offshoot from the Teleostoman stem which

TEXT-FIG. 88.
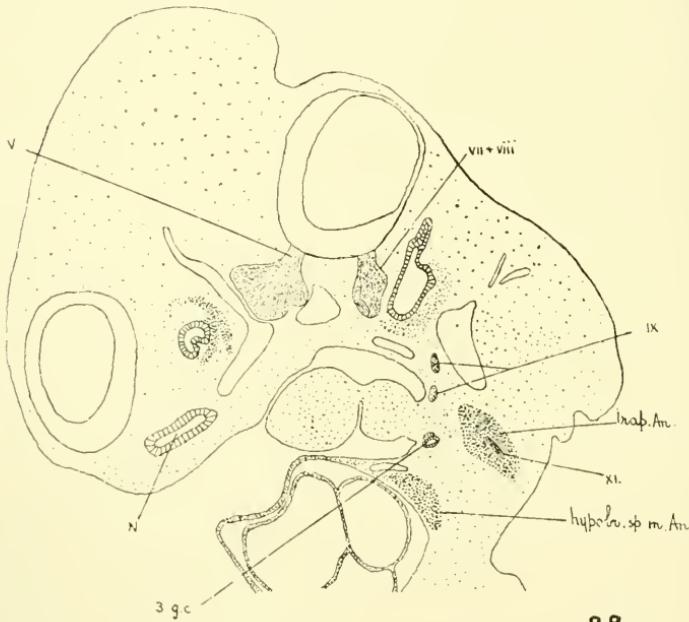
Rabbit, embryo 7 mm., longitudinal vertical section.

acquired an autostylic structure before the hyomandibula
had become very large and before the hyostylism had become
fully established." The non-division of the mandibular
myotome and the persistence of the dorso-ventral sheet
C_2vd are, however, more primitive features than exist in
Teleostomi; and in the embryo of Ceratodus there is
a hyomandibula, the relations of which are different from
those occurring in Teleostomi.

Graham Kerr's opinion was that "the Teleostomes the Dipnoans and the Amphibians have arisen in phylogeny from a common stem . . ."

Kellicott's statements that "the resemblances in the vascular system between Ceratodus (the most primitive of the living Dipnoi) and the Amphibia, especially Urodela, are numerous and fundamental and cannot be explained as parallelisms," and that "most of the Elasmobranch characters are parallelisms, some of them actually being preceded by Amphibian conditions (e.g. the carotid arteries)" are also true of the cranial muscles.

Consideration of the common features in the cranial muscles of Teleostoman embryos leads to the probability that some remote ancestors possessed—a mandibular myotome divided into upper and lower parts[1]; a levator hyoidei, which, owing to the upgrowth of the hyoid bar to the periotic capsule, was inserted into the inner or posterior surface of a hyomandibula; a dorso-ventral sheet in the opercular fold, divided into a M. opercularis and a constrictor operculi; a series of levatores arcuum branchialium; a trapezius developed from the fourth levator; a series of Mm. marginales not fused with the transversi ventrales; a series of hypobranchial-cranial muscles consisting of interarcuales ventrales and of a coraco-branchialis attached to the last branchial bar; hypobranchial-spinal muscles, consisting of a coraco-hyoideus, and of a genio-hyoid, the hind end of which had grown back to some more posterior branchial bar overlapping the coraco-hyoideus.

All these features, with five exceptions, may be supposed to have characterised primitive Amphibia; and these exceptions, viz. division of the mandibular myotome, formation of a M. opercularis, and of a coraco-branchialis, backward growth of the genio-hyoid, upward extension of the hyoid

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[1] On the supposition that the protractor hyomandibularis of Acipenser is a case of atavism in its non-division into levator arcus palatinus and dilatator operculi, this division of the levator maxillæ superioris would have once characterised the whole group.

F. H. EDGEWORTH.

TEXT-FIG. 89.

vii + viii

vii

An. of post. dig.
styloby + stap.

ant. dig. An.

interhyoid

89.

TEXT-FIG. 90

tr. my.

trap. An.

dor. aor.

hypolv. sb. m. An.

cœl.

œsoph.   trach.
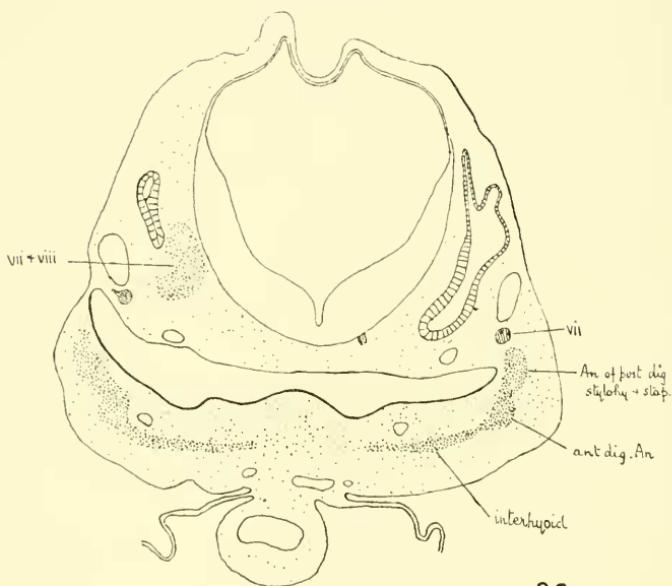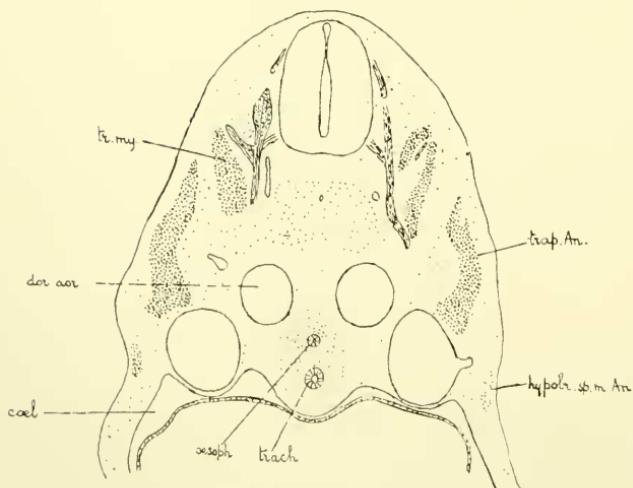
90.

Text-figs. 89 and 90.—Rabbit, embryo $7\frac{1}{2}$ mm.; Text-fig. 89 through
the hyoid segment. Text-fig. 90 through the neck.

bar to the periotic capsule—are, as shown by their develop-
ment, modifications of more primitive features existing in
Amphibia.

These phenomena may be considered as additional argu-
ments in favour of the theory of a descent of Teleostei, as
advocated by Assheton, from a proto-amphibian stock ; and
of Teleostomi in general, as advocated by Graham Kerr, from
a stem common to the Teleostomi, Dipnoi, and Amphibia.

In the condition of the cranial muscles Teleostei do not
show any closer resemblances to Amphibia than do other
groups of the Teleostomi.

The curious fact that the trapezius is developed from the
fourth levator arcuum branchialium in Acipenser, Lepidosteus,
Amia, and Salmo, though there are five branchial segments,
suggests that ancestors of the Teleostomi may have had, like
Amphibia, only four branchial segments, and that an increase
to five took place within the group.

In the possession of only four branchial segments, of
interarcuales ventrales I, II, and III, of obliquii ventrales
not fused with transversi ventrales, and of very primitive
laryngeal muscles, Polypterus senegalus shows closer
resemblances to Amphibia than do the other Teleostomi
examined.

The main characteristics of the cranial muscles of Selachii
are: (1) Division of the mandibular myotome into levator
maxillæ superioris and adductor mandibulæ ; (2) great
backward extension of the intermandibularis below the
interhyoideus ; (3) non-formation of an opercular fold ;
(4) upgrowth of the hyoid bar internal to the hyoid myotome,
which, originally forming a levator hyoidei, becomes inserted
into its external surface (hyomandibula, or this and
ceratohyal); (5) non-formation of a hyo-maxillaris ; (6)
extension backwards of hyoid myotome and interhyoideus
forming a dorso-ventral sheet C_2vd behind the hyoid bar,
though not in an opercular fold ; (7) non-formation of
levatores arcuum branchialum ; (8) formation of a trapezius
from the upper ends of all the branchial myotomes ; (9)

formation of subspinalis and interbasales from anterior trunk myotomes; (10) formation of coraco-branchiales; (11) formation of adductors from the portions of the branchial myotomes which lie internal to the branchial bars; (12) formation of arcuales dorsales, interbranchials, and superficial constrictors from the portions of the branchial myotomes which lie external to the branchial bars; (13) non-formation of transversi ventrales; (14) extension backward of the genio-hyoid, forming a coraco-mandibularis. Of these features, (3) (9) and (12) occur in Selachii and them only.

The great development of the branchial musculature, external to the branchial bars, is correlated with the absence, probably the loss, even in developmental stages, of an opercular fold. It is of interest to note that in Chimæra (Vetter) (1) a hyo-maxillaris (hyoideus inferior) is present; (2) the dorso-ventral sheet C_2vd is situated in an opercular fold; (3) the branchial musculature, external to the bars, consists of simple vertical muscles ("interbranchials" of Vetter), which are similar to the Mm. marginales of Anuran larvæ and Ceratodus, and to the dorsal portions of the obliqui ventrales of Teleostomi.

According to Graham Kerr, "the Teleostomes, the Dipnoans, and the Amphibians have probably arisen in phylogeny from a common stem, which would in turn probably have diverged from the ancestral Selachian stock." Fürbringer's theories in regard to the hypobranchial muscles and the neocranium, and Ruge's respecting the facial muscles, are also based on a similar theory.

Consideration of the morphology of the cranial muscles leads to some doubt on this question. The embryology of each group of cranial muscles, mandibular, hyoid, branchial, hypobranchial-cranial, and hypobranchial-spinal, suggests that the conditions found in Selachii are secondary to those which may be supposed to have characterised Amphibian ancestors—are modifications of a proto-amphibian type. Certain of these modifications occur in other groups also: thus division of the mandibular myotome into upper and lower

parts also occurs in Teleostomi and Sauropsida; backward extension of both hyoid myotome and interhyoideus to form a dorso-ventral sheet also occurs in Ceratodus and Teleostomi (though in these, in an opercular fold) formation of

TEXT-FIG. 91.
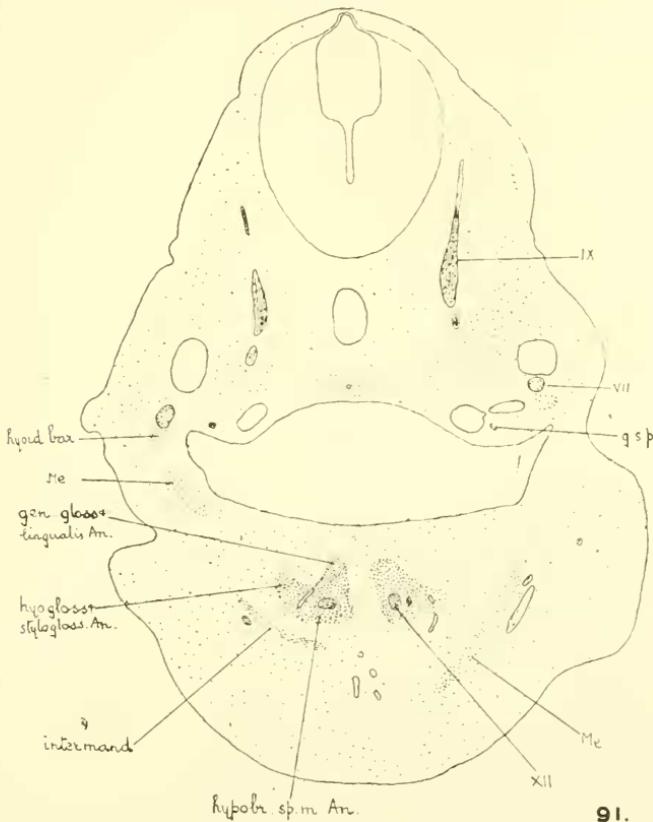
Text-figs. 91–93.—Rabbit, embryo 9 mm.; Text-fig. 91 through the mandibular segment, Text-figs. 92 and 93 through the hyoid segment.

coraco-branchiales and of a coraco-mandibularis also occurs in Ceratodus and some Teleostomi; non-formation of levatores arcuum branchialium, and the associated method of development of the trapezius occurs in Sauropsida and rabbit.

The significance of such resemblances from a phylogenetic point of view is doubtful, though probably the first two named are by far the most important.

The ancestry of Mammals has been the subject of inquiry and speculation for many years. Two theories have been
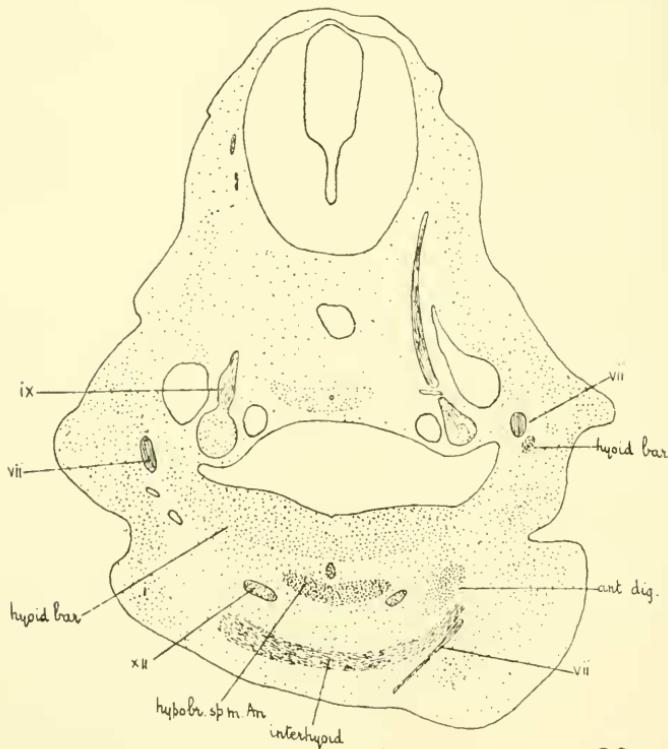
TEXT-FIG. 92.

held—one, that Mammals are descended from Sauropsida, the other, that they are descended from Amphibia.

As regards the cranial muscles, Mammals resemble Amphibia, and differ from Sauropsida in the following particulars: non-division of the mandibular myotome into dorsal and ventral parts, formation of a hyo-maxillaris (anterior digastric), non-formation of a dorso-ventral sheet

C_2vd in the hyoid segment, innervation of the interarcualis ventralis I (branchio-hyoideus) by the IXth.

On the other hand, Mammals resemble Sauropsida, and differ from Amphibia, in the non-formation of levatores arcuum branchialium, and the associated development of the

TEXT-FIG. 93.
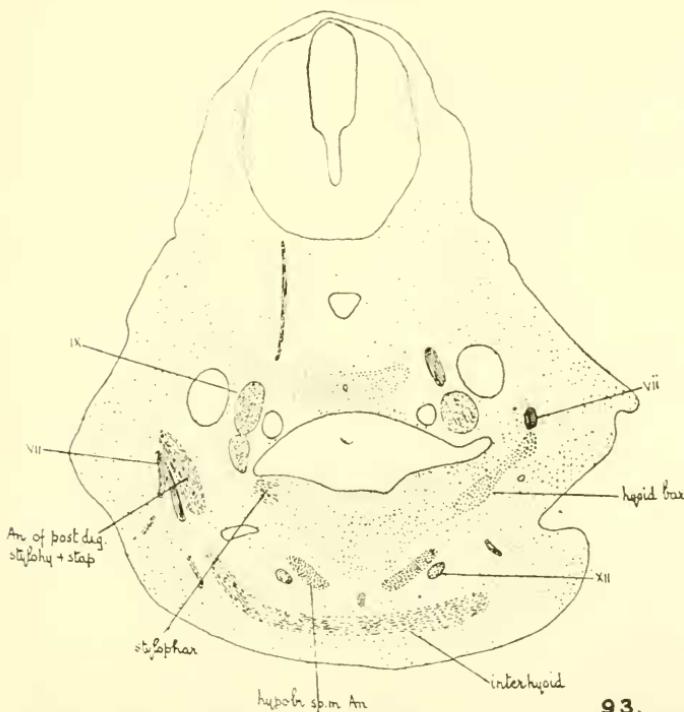
93.

trapezius from the upper ends of all the branchial myotomes, disappearance of the branchial myotomes (after formation of trapezius and interarcuales ventrales from their upper and lower ends), non-formation of transversi ventrales.

It has been suggested above in discussing individual groups of muscles that all the first-named features are primary ones, and that all the second-named features are secondary phenomena. It is possible that secondary features may have

been independently acquired; thus the absence of levatores
arcuum branchialium and method of formation of the
trapezius also occurs in Selachii. The morphology of the
cranial muscles is thus in favour of an Amphibian ancestry of
Mammals. In the attachment of the posterior digastric to
the hyoid bar, and not to the lower jaw, some Mammals
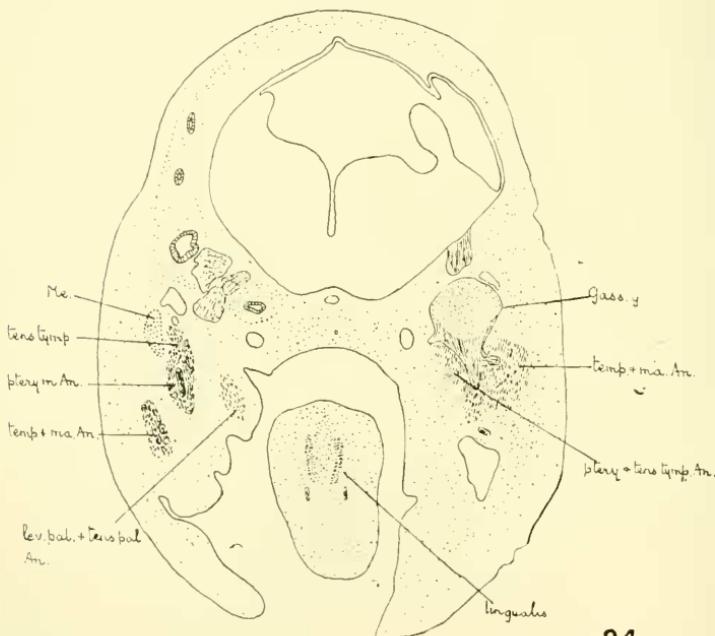
TEXT-FIG. 94.

Text-figs. 94 and 95.—Rabbit, embryo 13 mm.; transverse sec-
tions through the mandibular segment. Text-fig. 94 is the
more anterior.

present a more primitive feature than is found in any adult
Amphibia. A descent from a proto-amphibian stock is thus
suggested.

The ancestry of Sauropsida has been the subject of but
few speculations. Fürbringer was of opinion that "Die
strepto-stylen Pro-reptilia aber haben sich neben den strepto-
stylen Pro-mammalia auf tiefer stehenden streptostylen

Thieren entwickelt welche im Grade ihrer Ausbildung amphibienartige Thiere gleichzusetzen sind. . . ." Graham Kerr's opinion was that "the ancestors of the Amniota probably diverged about one or several points from the region of the stem common to Dipnoi and Amphibia."

As regards the cranial muscles, the differences between

TEXT-FIG. 95.
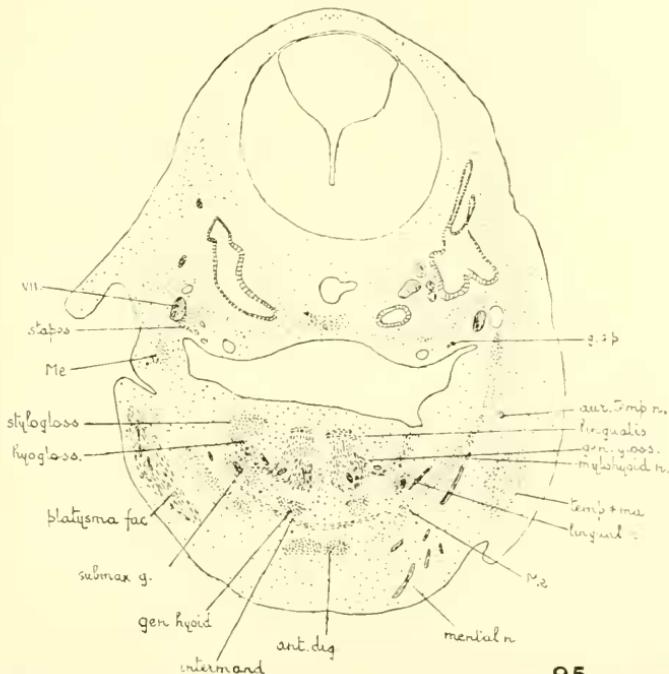
Sauropsida and Amphibia have been mentioned above. In the division of the mandibular myotome into upper and lower portions, and in the formation of a ventro-dorsal sheet, C_2vd, in the hyoid segment, Sauropsida resemble Selachii and Teleostomi, and also as regards C_2vd, Dipnoi. The shifting of insertion of the levator hyoidei from cerato-hyal to Meckel's cartilage and the morphologically primitive condition of the hypobranchial spinal muscles are common to both Sauropsida and Amphibia.

On Fürbringer's Theory of the Skull.

It is of interest to inquire whether the above suggestions as to the phylogeny of various groups of Vertebrates receive any support from the morphology of the skull.

According to Fürbringer's theory the portion of the cranium in front of the exit of the vagus is the original cranium—the palæocranium. The neocranium has been formed by the addition of spinal skeletal elements, which originally were free. This took place in several stages ; in the first a proto-metamer neocranium is formed—present in Selachii and Amphibia. The union of further additional elements brings about the auximetamer condition of the neocranium, found in higher fishes and Amniota.

The added spinal nerves—spino-occipital nerves—can be divided into two categories, the " occipital," brought in with the protometamer neocranium, and the " occipito-spinal," additionally added with the auximetamer neocranium. The varying number of spino-occipital nerves is due to the varying position of the cranio-vertebral junction.

The assimilated occipital nerves are indicated by the terminal letters of the alphabet, the assimilated occipito-spinal nerves by the initial letters. Their corresponding myotomes are given corresponding (larger) letters. By this method it is possible to express either or both of two possi-bilities—the reduction of more anterior or the addition of more posterior nerves.

The following table, which is taken mostly from Gaupp, shows the results of the investigation of various vertebrates, and a column has been added showing the number of myotomes taking part in the formation of the hypo-branchial muscles.

A spinal segment is typically indicated by a somite or myotome, anterior nerve root, and posterior nerve root. The researches of Fürbringer and other observers have shown that as segments are assimilated their nerve roots tend either not

|	No. of trunk segments taken up into the skull.	Nature of neocranium according to Fürbringer's theory.	Taking part in the formation of hypobranchial spinal muscles.
Anura—			
Pelobates (Sewertzoff)	3	Protometamer	—
Rana (Miss Elliott)	3	,,	1st, 2nd.
Urodela—			
Siredon (Sewertzoff)	2	,,	—
Necturus (Miss Platt)	3	,,	2nd (few cells), 3rd, 4th, 5th (Miss Platt).
Triton	—	—	—
Dipnoi—			
Ceratodus (K. Fürbringer)	5	Anximetamer (Gaupp)	2nd 3rd (Greil).
Protopterus (Agar)	3	Protometamer (Agar)	2nd, 3rd, 4th (Agar).
Lepidosiren (Agar)	3	Ditto	2nd, 3rd, 4th (Agar).
Mammals—			
Sheep, calf (Froriep)	3	Anximetamer	—
Rabbit	—	,,	1st, 2nd, 3rd.
Reptilia—			
Ascalobates (Sewertzoff)	4	,,	—.
Lacerta (Hoffman)	5	,,	2nd, 3rd, 4th, 5th (Hoffman)
Lacerta (Chiarugi and v. Bemmelen).	4	,,	—
Birds—			
Tinnunculus (Suschkin)	4	,,	—
Gallus	—	,,	1st (few cells), 2nd, 3rd, 4th, 5th.
Teleostomi—			
Amia (Schreiner)	4	,,	2nd, 3rd, 4th.
Salmo salar (Wilcox)	5	,,	2nd, 3rd, 4th (Harrison).
Trutta fario (Wilcox)	5	,,	—
Lepidosteus (Schreiner)	7	,,	2nd, 3rd, 4th.
Acipenser (Sewertzoff)	7	,,	2nd, 3rd, 4th.
Selachii (Gaupp)—	7	Protometamer	—
Squalus acanthias	—	,,	4th, 5th, 6th, 7th, 8th (Neal).
Scyllium canicula	—	,,	4th, 5th, 6th, 7th, 8th.

to be developed, or after development to atrophy, and that
this takes place from before backwards. The non-development
ment or atrophy affects dorsal more readily than ventral
roots. Reduction, i.e. atrophy after development, of somites

or myotomes comes last. This general rule leads to hesitation in accepting the existence of anterior nerve roots without corresponding somites or myotomes as evidence of assimilated segments, e.g. deductions from the observations of Chiarugi and Martin in Mammals.

The theory of Fürbringer is based on the probability of the primitive nature of the conditions found in Selachians. But from the foregoing table of the observed number of assimilated spinal segments in various Vertebrates it would appear that the descriptive adjectives applied to some neocrania are not deserved. As determined by the number of assimilated spinal segments the Amphibian neocranium is shorter than that of Selachians. It was therefore maintained that the occipital region of Amphibians corresponds to a multiplum of spinal segments. The difficulty of doing so is emphasised by the absence of any direct evidence in its favour. If the muscles of the head in Amphibians and Selachians be compared it is clear that the condition in the former is far more primitive than in the latter, and that many cranial muscles of Scyllium pass through what may be regarded as an Amphibian stage during development; and if the observed facts in regard to the number of assimilated spinal segments be taken sans parti pris the condition of the skull tells the same tale. Fürbringer states that the junction of the skull and vertebral column is at the same place in Sauropsida and Mammalia; hence the five occipital nerves in Reptilian embryos are called v, w, x, y, z; and the three in Mammals x, y, z, so that the last assimilated nerve is the same—z. But in Mammals there appear to be only three assimilated somites, in Reptiles four or five. The argument drawn from the existence of a pro-atlas is probably of no great weight in determining the limits of the skull and vertebral column, for in Sphenodon (loc. cit.) that structure is the persisting costal process of the last coalescing vertebra, and the same may be true in Mammals without there being any but a serial homology between these last coalescing vertebræ.

The conclusion which might be drawn from the number of

TEXT-FIG. 96.
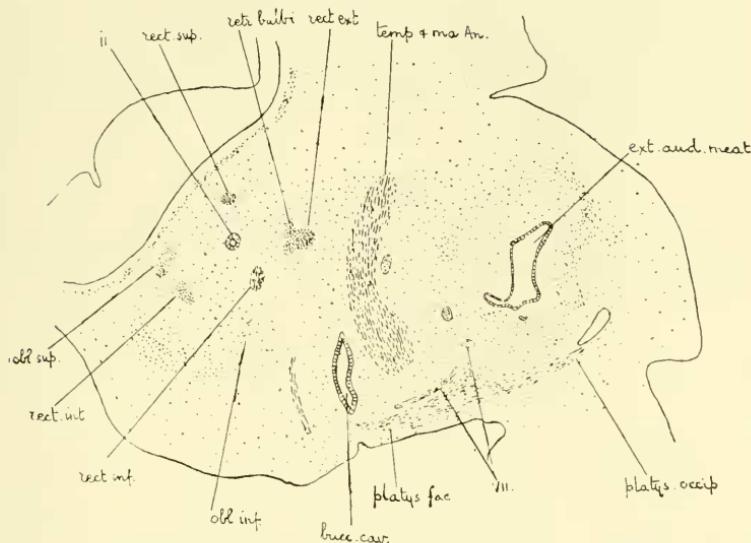
96.

TEXT-FIG. 97.
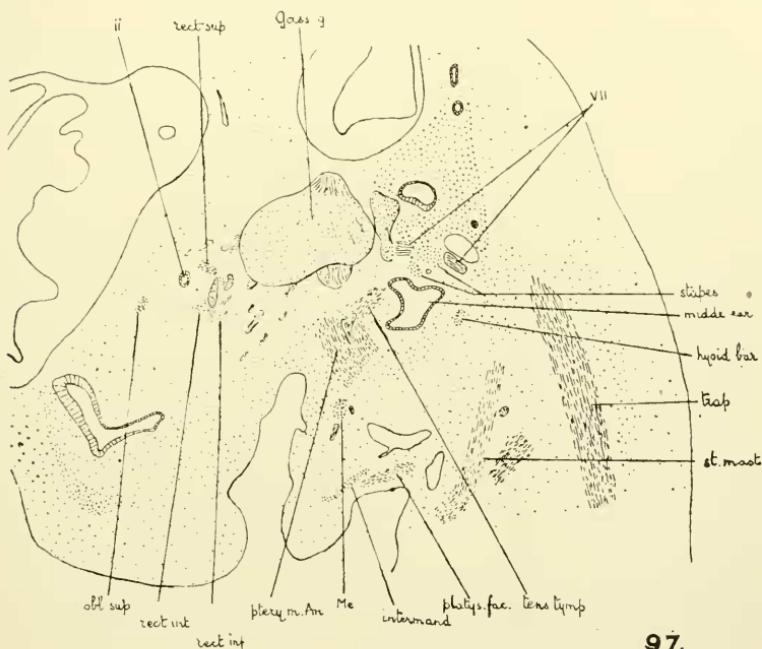
97.

Text-figs. 96 and 97.—Rabbit, embryo 13 mm., longitudinal vertical
sections. Text-fig. 96 is the more external.

coalescing spinal segments in Amphibia, Sauropsida, and Mammalia—viz. 2 or 3, 4 or 5, and 3—harmonises with the evidence of the cranial muscles, in which there is a closer similarity between Mammalia and Amphibia than between Mammalia and Sauropsida.

A Suggested Morphological Classification of the Motor Centres of the Mid- and Hind-Brain in Man.

Gaskell divided the motor centres of the cranial nerves
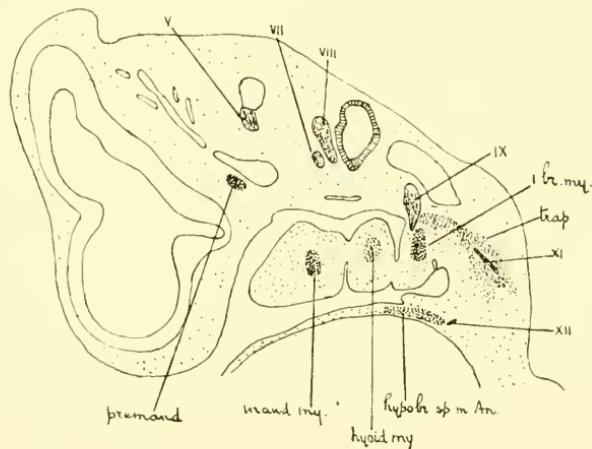
Text-fig. 98.

Pig. embryo 8 mm., longitudinal vertical section.

into two categories : (1) Somatic, a continuation of the anterior column of the spinal cord, innervating somatic muscles—IIIrd (external ocular muscles), IVth, VIth, VIIth (part which arises from the VIth nucleus), XIIth. (2A) Non-ganglionated splanchnic, a continuation of the lateral column of the spinal cord, innervating voluntary splanchnic muscles—Vth (motor descending root), Vth (motor), VIIth, IXth, Xth, XIth (part which arises from lateral horn). (2B) Ganglionated splanchnic, a continuation of Clarke's column—IIIrd (G. ciliare), VIIth (N.

intermedius with gang. genic.), IXth (gang. petros.), Xth, XIth (gang. trunci vagi), XIIth (gang. hypoglossi).

This classification of the motor centres, as regards those of voluntary muscles, followed v. Wijhe's theory of the morphology of the cranial muscles. It was also adopted by Strong and by Herrick.

According to Streeter the motor nucleus of the Vth nerve in man is developed in the lateral plate, and the nucleus ambiguus of the VIIth, IXth, and Xth in the basal plate.
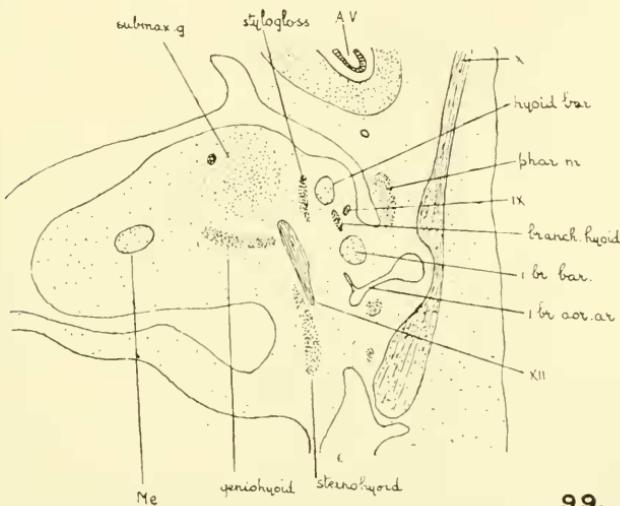
TEXT-FIG. 99.

Pig, embryo 15 mm., portion of longitudinal vertical section.

The issuing fibres of the Vth pass straight outwards like those of the dorsal efferent fibres of the IXth, Xth, and XIth (medullary) ; whilst those of the VIIth, IXth, and Xth, arising from the nucleus ambiguus, have a characteristic curved path. The motor nucleus of the Vth is a hypertrophied representative of the dorsal motor nuclei of the IXth, Xth, and XIth (medullary), or the latter is represented in the mesencephalic root of the Vth.

Kappers showed that the original position of the VIIth, IXth, and Xth motor nuclei is medio-dorsal, and that the

ventral position of the nucleus ambiguus is only found in
Mammals, where the importance of the ventral tegmentum
is increased by the pyramidal tract, whilst a part keeps its
original position near the mid-dorsal line because not very
much influenced by the long descending tracts of the frontal
parts of the brain.

It would result from a comparison of these researches that
the ventral position of the VIIth nucleus, and of the nucleus
ambiguus of the IXth and Xth, is a secondary one, the curved
path of their issuing fibres representing a phylogenetic descent
of the whole or part of their nuclei ; whilst the motor nucleus
of the Vth has preserved its original position. This position
is a dorso-median one. The nucleus of the XIth spinal
occupies a more or less lateral position in the cervical cord,
but, as shown by the development of the muscles it inner-
vates, the nerve is a specialised branch of the Xth, the
nucleus of which has extended backwards into the spinal cord.

The following classification of the motor nuclei of the
cranial nerves is a repetition from a neurological point of
view of the theory which has been advanced above concern-
ing the morphology of the cranial muscles, and consequently
stands or falls with it.

Somatic, innervating muscles derived from the myotomes
of the cerebral and three anterior body segments ; IIIrd
(external ocular muscles), IVth (superior oblique), VIth
(external rectus), Vth (temporal, masseter, pterygoids, tensor
tympani, anterior digastric), VIIth (posterior digastric, stylo-
hyoid, stapedins), IXth (interarcualis ventralis I s. branchio-
hyoideus, when present), Xth and XIth medullary (inter-
arcualis ventralis III s. interthyroideus, in Ornithodelphia),
XIth spinal (sterno-mastoid and trapezius), XIIth (hypo-
branchial spinal muscles, and lingual muscles derived from
the genio-hyoid). Splanchnic, innervating muscles derived
directly or indirectly from the walls of the cephalic cœlon,
i. e. part of motor nucleus of Vth, which innervates mylohyoid;
part of motor nucleus of VIIth, which innervates facial and
platysma muscles; part of motor nuclei of IXth, Xth, and

XIth medullary, which innervates tensor and levator palati, palato-glossus, stylopharyngens, pharyngeal constrictor, laryngeal muscles, crico-thyroid.

The primary cranial nerves are the IIIrd, Vth, VIIth, IXth, and Xth; the Xth innervating in the rabbit two myotomes (second and third branchial), the others one each. The primary dorsal position of their motor nuclei (other than that of the IIIrd), the dorso-lateral emergence of their motor with their sensory fibres, and the relationship—external—of the issuing nerves to the corresponding myotomes, are related phenomena. If Balfour's theory, that the head and trunk became "differentiated from each other at a stage when mixed dorsal and sensory posterior roots were the only roots present," be associated with Fürbringer's theory that the myotomes primitively lay exclusively lateral to the notochord, it would follow that in the body region anterior nerve roots were secondarily developed in correlation with the upgrowth of the myotomes to the mid-dorsal line, and the posterior roots became exclusively, or almost exclusively, sensory. In the head, where this upgrowth does not take place, or to a very limited extent, a more primitive condition persists both in the position of the motor nuclei and the emergence of their efferent fibres.

A further, probable, distinction between the somatic muscles of the body and those of the head is that ganglionated muscle-sensory nerve-fibres pass to the former but not to the latter.[1]

The position of the nucleus of the IIIrd nerve and the path of its nerve-fibres may be associated with the loss of cutaneous sensory fibres. Evidence of such loss and of a primitive dorso-lateral emergence of its nerve-fibres is found in the observation of Neumeyer that in the twenty-nine and forty-three hours old chick "der Nerf vom dorsalen Theile des Mittelhirns, also in der Gegend der Ganglionleiste seinen Ursprung nehme, sich also sekundär mit seinem definitiven Abgangsort vereinige."

[1] I hope to give the evidence for this in a future paper.

The Anlagen of the superior oblique and external rectus are developed from forward extensions of the upper ends of the mandibular and hyoid myotomes, and the IVth and VIth nerves may be regarded as, phylogenetically, late formations.

There do not appear to be any investigations on the existence of cell-groups in the Vth motor nucleus, which might correspond to the somatic and splanchnic muscles innervated. The nucleus contains a centre for the anterior digastric, but it is not known whether this migrates, during development, from the facial nucleus, or whether it is locally developed. The fibres of the Vth mesencephalic root join the motor root (Cajal), but it does not appear certain what structures it innervates.

The motor nucleus of the VIIth nerve consists, according to van Gehuchten and Marinesco, of four cell groups, three ventral and one dorsal : of these, the internal ventral is the centre for the stapedius, the middle for the auricular muscles, the external for the inferior facial muscles, and the dorsal nucleus for the superior facial muscles (frontalis, corrugator supercilii, and orbicularis palpebrarum). According to this account there is no special cell-group for the posterior digastric and stylohyoid, which seems unlikely. More recently, Kosaka has stated that the dorsal cell group in the fowl is the motor nucleus for the digastricus. The subject evidently needs further investigation.

The glosso-pharyngeal nucleus, according to v. Gehuchten, consists of a ventral cell-group only ; according to Streeter it has a dorsal nucleus as well as a nucleus ambiguus. In the monkey (Beevor and Horsley) it innervates the stylopharyngeus and (?) the middle constrictor of the pharynx. It is not known whether there is a separate cell-group for the branchio-hyoid in animals, e. g. pig, dog, where this muscle exists.

The Xth and XIth medullary are primitively, in the rabbit, the nerves of the second and third branchial segments. The Xth efferent fibres arise from dorsal and ventral motor nuclei, those of the XIth medullary from a dorsal nucleus only (v.

Gehuchten). As all the fibres of the XIth medullary join the Xth, and all the fibres of the XIth spinal pass to the trapezius and sterno-mastoid,[1] it is a little questionable whether the old distinction of the two parts of the accessorius is worth preserving. The term XIth or accessorius might well be limited to what is now known as the XIth spinal. In a Mammal like the rabbit, where the whole of the second and third branchial myotomes (other than their dorsal ends which take part in forming the trapezius and sterno-mastoid) disappear during development, the Xth and XIth medullary motor centres contain none of the original somatic efferent fibres or cell-groups, and their new centres are those innervating muscles derived from cells proliferated from the wall of the cephalic coelom. They also contain motor centres for certain visceral muscles which are developed in the body region.

The Xth and XIth medullary centres overlap antero-posteriorly the hypoglossal nucleus, probably owing to their backward extension into the first three segments of the spinal cord.

The XIth spinal is, as emphasised by Fürbringer, a true cerebral and not a spinal nerve. It innervates a special group of muscles which, in the rabbit, are derived from the upper ends of the three branchial myotomes. Its nucleus of origin is, from a phylogenetic point of view, a backward extension into the spinal cord of the (dorsal) nucleus of the XIth medullary, but it is not known what happens in embryonic development.

The hypoglossal nucleus is the motor centre of the hypo-branchial spinal muscles, of the rectus system, developed from the first three body myotomes. Cell-groups corresponding to the upper, atrophying portions of these myotomes have been lost. It is not known whether the subdivision of the nucleus into the parts with large and with moderate-sized cells corresponds with individual muscles or muscle-groups. The hinder part of the hypobranchial spinal muscles has a

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[1] In dog (loc. cit.) and man (Streeter).

secondary innervation from cervical segments—first, second, and third in man, first and second in the dog—but it is not known whether this is due to backward migration or to local development of motor neuroblasts.

On the Size of the Medullated Nerve-Fibres Passing to Cranial Muscles.

Gaskell stated that in the dog large fibres, 14·4 to 18 μ in diameter, were present in the IIIrd (external ocular muscles), IVth, VIth, VIIth (destination not traced), and XIIth. The corresponding muscles were considered to be somatic. Nerve-fibres not exceeding 10·8 μ in diameter were found in VIIth (facial muscles), pharyngeal nerves, and recurrent laryngeal; and the corresponding muscles were considered to be splanchnic. Apparently he did not take the size of the nerve-fibres as the sole criterion of the somatic or splanchnic nature of a muscle, for the sterno-mastoid and trapezius were considered to be splanchnic, though the nerve (spinal XIth), showed the larger size of nerve-fibres. A further analysis (loc. cit.) of the size of nerve-fibres passing to cranial muscles in the dog shows that : (1) In any individual nerve, fibres are found of all sizes up to the largest present; (2) the nerve-fibres taper very slightly as they pass from the central nervous system to the muscles; (3) if comparison be made between the maximum size of the nerve-fibres and the morphological nature of the muscles to which they pass, the following results appear : (A) Nerve-fibres of the greatest size (17·6 μ in diameter,[1] in some dogs only 16 μ), are found in the nerves of the external ocular muscles, temporal, pterygoids, tensor tympani, digastric (both from Vth and VIIth), stylo-hyoid, branchio-hyoid, trapezius, sterno-mastoid, genio-hyoid, sterno-hyoid, sterno-thyroid, thyro-hyoid, and omohyoid—all of which, according to the theory

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[1] This is also the maximum size of the nerve-fibres in the anterior roots of the non-limb portions of the spinal cord. In the limb areas it is slightly greater.

advanced above, are somatic in origin. (B) Nerve-fibres of a less maximum diameter (12·8 μ, in some dogs only 11·2 μ), are found in the nerves of the mylohyoid, facial and platysma muscles, palatal, pharyngeal, and laryngeal muscles and crico-thyroid — all of which, according to the theory advanced above, are splanchnic in origin; and also in the nerves of the lingual muscles, which are developed from the genio-hyoid—a somatic muscle.

Herrick stated that the nerve-fibres of the branchial muscles of Menidia were characterised by their large size, and supposed—on the theory that these muscles were of splanchnic origin — that they had acquired this somatic feature. On the theory advanced above, however, the bran-chial muscles are somatic in origin.

The small size of the nerve-fibres of the lingual muscles is curious, but the muscles, though somatic in origin, have intimate relations to a splanchnic epithelium. This sugges-tion is supported by the measurements of the nerve-fibres passing to the genio-hyoid and lingual muscles of Lacerta viridis and Testudo mauritania; in the former animal the maximum diameters found are 11·6 and 9·6 μ respectively, whereas in the latter animal both maxima are the same, viz. 7·5 μ.

I have, in conclusion, to express many thanks to Prof. Salensky for embryos of Acipenser; to Prof. Bashford Dean for embryos and for the loan of sections of Ceratodus; to Prof. Graham Kerr for specimens of Polypterus senegalus; and to Prof. Fawcett for the loan of sections of the pig; also to the last-named for much kindness shown to me during many years in his laboratory.

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EXPLANATION OF REFERENCE LETTERS ON THE TEXT-FIGURES.

abd. An. Abducens Anlage. *An. of sup. obl.* Anlage of obliquus superior. *abd. hyoid.* M. abdomino-hyoideus. *add. mand.* M. adductor mandibulæ. *add. mand. ext.* M. adductor mandibulæ externus. *add. mand. int.* M. adductor mandibulæ internus. *ant. dig.* M. digastricus

anterior. *arcualis dors*. M. arcualis dorsalis. *aur. temp. n*. Auriculo-temporal nerve. *br. add*. M. adductor arcus branchialis. *br. aor. ar*. Branchial aortic arch. *br. bar*. Branchial bar. *br. my*. Branchial myotome. *branch. hyoid*. M. branchio-hyoideus. *bucc. cav*. Buccal cavity. *ceph. cœl*. Cephalic cœlom. *cer. br*. Cerato-branchial cartilage. *cer. hy. ang*. M. cerato-hyoideus angularis. *cer. hyal. c*. Cerato-hyal cartilage. *first cerv. n*. First cervical nerve. *cœl*. Cœlom. *cons. colli*. M. constrictor colli. *cons. operc*. M. constrictor operculi. *cor. branch*. M. coraco-branchialis. *cor. hyoid*. M. coraco-hyoideus. *cor. mand*. M. coraco-mandibularis. *c₂vd*. Dorso-ventral muscular sheet in hyoid segment. *dil. lary*. M. dilatator laryngis. *dilat. operc*. M. dilator operculi. *dor. aor*. Dorsal aorta. *dorso-lary*. M. dorso-laryngeus. *epibr*. Epibranchial cartilage. *ext. aud. meat*. External auditory meatus. *extra-temp*. M. extra-temporalis. *Gass. g*. Gasserian ganglion. *gen. glossus*. M. genio-glossus. *gen. glossus and lingualis an*. Anlage of M. genio-glossus and lingualis. *gen. hyoid*. Genio-hyoid. *gill. m. An*. Anlage of muscles of external gill. *g.-c*. Gill-cleft. *hy. ceph. cœl*. Hyoid section of cephalic cœlom. *hyogloss*. M. hyo-glossus. *hyogloss. and stylogloss. An*. Anlage of M. hyoglossus and M. styloglossus. *hyohy. inf*. M. hyo-hyoideus inferior. *Hyohy. sup*. M. hyo-hyoideus superior. *hyoid bar*. Hyoid bar. *hyoid my*. Myotome of hyoid segment. *hyoid aor. ar*. Hyoid aortic arch. *hyomax*. M. hyomaxillaris. *hyomax. lig*. Hyomaxillaris ligament. *hyomand. c*. Hyomandibular cartilage. *hypobr. c*. Hypobranchial cartilage. *hypohyal*. Hypohyal cartilage. *hypobr. sp. m. An*. Anlage of hypobranchial spinal muscles. *inf. lab. cart*. Inferior labial cartilage. *interarc. vent*. M. interarcualis ventralis. *interbas*. M. interbasalis. *interhyal*. Interhyal cartilage. *interhyoid*. M. interhyoideus. *intermand*. M. intermandibularis. *lary*. Larynx. *lev. br*. M. levator arcus branchialis. *lev. hyoid*. M. levator hyoidei. *lev. lab. sup. An*. Anlage of M. levator labii superioris. *lev. max. sup*. M. levator maxillæ superioris. *lev. pal. and tens. pal. An*. Anlage of levator and tensor palatini. *lingualis*. M. lingualis. *M. marg*. M. marginalis. *mand. aor. ar*. Mandibular aortic arch. *mand. ceph. cœl*. Mandibular section of cephalic cœlom. *mand. lab*. M. mandibulo-labialis. *mand. my*. Myotome of mandibular segment. *mand. seg*. Mandibular segment. *mass*. M. massetericus. *mylohyoid n*. Mylohyoid nerve. *Me*. Meckel's cartilage. *mental n*. Mental nerve. *N*. Olfactory epithelium. *nictat. m. An*. Anlage of nictating muscles. *obliq. dors*. M. obliquus dorsalis. *obliq. inf*. M. obliquus inferior. *obliq. sup*. M. obliquus superior. *obliq. vent*. M. obliquus ventralis. *œsoph. const*. Constrictor of œsophagus. *oper. fld*. Opercular fold. *orb. hyoid*. M. orbito hyoideus. *pal. pr. of quad*. Palatine process of quadrate. *pal. quad*. Palato-quadrate. *pal. quad. Me*. palato-quadrato-mandibular arch. *phar*. Pharynx. *phar. br*. Pharyngo-branchial cartilage. *phar. clav. ext*. M. pharyngo-clavicularis externus. *phar. clav. int*. M. pharyngo-clavicularis

internus. *phar. m.* Pharyngeal muscles. *platys. colli.* Platysma colli. *platysma fac.* Platysma faciei. *platys. occip.* Platysma occipitalis. *premand. An.* Anlage of premandibular muscles. *post. dig., stylohy. and stap. An.* Anlage of posterior digastric stylohyoid and stapedius muscles. *proc. asc.* Processus ascendens of quadrate. *proc. bas.* Processus basalis of quadrate. *protr. hyom.* M. protractor hyomandibularis. *ptery.* M. pterygoideus. *quad.* Quadrate. *quad. ang.* M. quadrato-angularis. *rec. lary. n.* Recurrent laryngeal nerve. *rect. ext.* M. rectus externus. *rect. inf.* M. rectus inferior. *rect. int.* M. rectus interior. *rect. sup.* M. rectus superior. *retr. arc. br.* M. retractor arcuum branchialium. *retr. bulbi.* M. retractor bulbi. *retr. hyom.* M. retractor hyomandibularis. *retr. hyom. et operc.* M. retractor hyomandibularis et opercularis. *scap.* Scapula. *sh. girdle.* Shoulder girdle. *spl. meso.* Splanchnic mesoderm. *st. mast.* M. sterno-mastoideus. *sterno-hyoid.* M. sterno-hyoideus. *stylogloss.* M. styloglossus. *stylophary.* M. stylopharyngeus. *submax.* M. submaxillaris. *submax. g.* submaxillary gland. *subment.* M. submentalis. *suborb. c.* Suborbital cartilage. *subtemp.* M. subtemporalis. *susp. ang.* M. suspensorio-angularis. *temp.* M. temporalis. *temp. and mass. An.* Anlage of M. temporalis external pterygoid masseter. *tensor tymp.* M. tensor tympani. *trach.* Trachea. *trap.* M. trapezius. *tr. my.* Trunk myotome. *trans. vent.* M. transversus ventralis. *vent. aor.* Ventral aorta. *Roman numerals.* Cranial nerves.